The Future of Southern Periphery Canada Lynx (*Lynx canadensis*): Habitat Suitability Projections for Lynx in the Washington-British Columbia Transboundary Region

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Abstract

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The Canada lynx (*Lynx canadensis*) is a medium-sized cat that preys primarily on snowshoe hares (*Lepus americanus*). As a species threatened in the contiguous U.S. that is dependent on climate-sensitive environmental conditions, lynx are vulnerable to climate change at southern range peripheries like those in Washington State. Present uncertainties limiting a clearer understanding of possible outcomes under climate change for lynx populations in the Washington-British Columbia (BC) transboundary region include knowledge gaps in understanding of regional-scale, habitat-selection drivers and in understanding of how these drivers translate to environmental predictors expected to change under climate.

To shed light on these knowledge gaps and to identify the possible range of climate impacts, I used the species distribution modeling program MAXENT to construct regional-scale core- and travel-habitat suitability models for the Washington-BC transboundary region. I then used MAXENT to project the core habitat suitability model to eighteen future climates projected for the 2020s, 2050s, and 2080s under six different climate scenarios. Results point to differences

between habitat selection at regional scales and that at local and broad scales. Relationships in the travel-habitat model suggest dispersal plasticity in lynx. Consistent with projections for lynx done at broad scales, projections for future climates unanimously indicated a northward range shift and increased habitat fragmentation over time. Though highly variable, all scenarios predicted loss of all suitable habitat cores in Washington State by the 2050s, and most predicted loss of all cores within the transboundary study area by the 2080s. My projections offer finer-resolution delineation of potential outcomes for lynx in this region than any previous analyses, characterization of uncertainties in climate futures that managers can use to contextualize likely changes, and a baseline that informs effective management for southern periphery lynx in this area going forward.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

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CHAPTER 1. HABITAT PROJECTIONS FOR CANADA LYNX IN THE WASHINGTON-BRITISH COLUMBIA TRANSBOUNDARY REGION: BACKGROUND AND OBJECTIVES

Introduction

Project Overview and Significance

Although natural changes and disturbances such as forest encroachment, over-exploitation, and introduction of invasive species have driven extinctions in the past, the magnitude of climate change projected for future decades introduces a new, unprecedented paradigm of change to climate-adapted landscapes (Pacifici et al. 2015). Research suggests that climatic shifts are not only already correlated with species responses, but also that these shifts may become a leading cause of biodiversity loss (Pacifici et al. 2015). As climate changes, metapopulation responses at species' southern range margins is projected to be slower than that at northern range margins (Anderson et al. 2009), leaving southern populations more vulnerable to climate change. Because changing climate modifies temperature and moisture dynamics within landscapes, it is expected to alter the relationships between these landscapes and the animals that use them, particularly for sensitive species whose preferences and requirements are tied to climatic gradients (Pacifici et al. 2015). The need for scenario-based assessments is clear. Ideal climatic envelopes for wildlife are shifting, frequently to higher latitudes or altitudes (Holderegger and Wagner 2008, Urban et al. 2013), and landscapes are projected to continue to change rapidly relative to historical rates (Schloss et al. 2012). This expectation raises questions as to how climate change will impact habitat suitability, habitat connectivity, population viability, and population dynamics of sensitive species at southern range peripheries, such as the Canada lynx (*Lynx canadensis*). The

Canada lynx (hereafter “lynx”), a medium-sized cat that preys primarily on snowshoe hares (*Lepus americanus*), is a threatened species in the contiguous United States (U.S.). Populations in Washington State exist in habitats that are already fragmented due to development, timber harvesting, and fires (Agee 2000, Koehler et al. 2008, Maletzke et al. 2008).

The picture for Washington State lynx populations appears dire, with atypical fire severity over the last several decades increasing habitat fragmentation and reducing lynx populations, though possibly temporarily (Koehler et al. 2008, Maletzke et al. 2008, Vanbianchi 2015). The level of uncertainty surrounding the potential impacts of changing climate is high, leaving the degree to which management will be effective in remediating these changes also uncertain. Clearer knowledge of the possible outcomes and the factors most strongly tied to them are integral to managing lynx under climate change and to identifying research needs. Uncertainties include large knowledge gaps in understanding of regional-scale, habitat-selection drivers, in how these drivers translate to environmental predictors expected to change with climate, and in how climate change is likely to affect habitat suitability of southern-periphery lynx populations in the Washington-British Columbia (BC) transboundary region. Uncertainty in climate projections makes not only the outcomes themselves uncertain, but also any course of remedial action. No analyses to date have been able to show what the regional-scale range of effects on habitat suitability might be or how the range of outcomes could vary.

This project is a regional, quantitative, and species-specific evaluation of the possible effect of projected changes and informs conservation in the face of them. Here I develop a transboundary regional-scale habitat suitability model for the Okanogan-BC transboundary region (*Chapter 2*) and project potential habitat suitability to future climates characterized by different climate scenarios to shed light on these knowledge gaps (*Chapter 3*). *Chapter 1* provides the baseline for this analysis, including providing the justification, significance, and an overview of the previous knowledge that informed decisions. A thorough literature review of the focal species' natural history and ecology is provided along with the starting-point objectives and summaries of the relevant issues and analyses. In developing habitat suitability models, I explore models, using model selection and tuning to determine the most appropriate models for both core- and travel-habitat suitability (*Chapter 2*). After projecting potential suitable habitat to future climates, I evaluate core habitat and range area for overall trends, differences in impact, and uncertainty, with a special focus on outcomes for lynx in Washington State (*Chapter 3*). Finally, I explore model limitations and caveats with respect to their ability to change projected outcomes and identify management considerations and conservation applications (*Chapter 3*).

Vulnerability to Climate Change

Species or populations that may face decline, reduced fitness, genetic loss, or extinction due to climate change are considered vulnerable (Dawson et al. 2011). There are three components that should be considered in assessing the vulnerability of a species or population to climate change: exposure, sensitivity, and adaptability (Dawson et al. 2011). Exposure is the magnitude of change likely in the habitat or region occupied by the species. Sensitivity refers to the degree to which a species' ability to persist is dependent on continuation of the prevailing climate and can depend on ecophysiology, life history, and microhabitat preferences. Finally, adaptability is the ability of the species or population to adjust to climate change. Adaptive responses can include "persisting in situ", and shifting locally or migrating to more suitable conditions. This analysis focuses primarily on exposure, by projecting suitability under a range of future climate scenarios, and sensitivity, by identifying environmental conditions lynx are dependent on that are sensitive to changing climate.

Global mean temperatures have increased in the past half century (IPCC 2013). In the last 1,400 years, the time period from 1983-2012 in the Northern Hemisphere was likely the warmest 30-year period (Alexander et al. 2013). In the Pacific Northwest, long-term warming trends are evident in observational datasets describing regional annual mean temperatures (Abatzoglou et al. 2014). In fact, very few years since 1980 have been below average annual mean temperatures (Abatzoglou et al. 2014). Positive trends in spring precipitation are also observed (Abatzoglou et al. 2014).

Populations of Canada lynx in Washington State are vulnerable to climate change for several reasons: (1) lynx habitat in Washington State is heavily fragmented, (2) habitats in Washington State are at the southern range periphery of the species' range, and (3) lynx preferences and requirements are tied to climatic gradients. Research suggests that lynx populations on the southern range periphery have already contracted northward by 22% of their historical range in Alberta, Canada (Bayne et al. 2008) and by 39% of their historical range overall (Laliberte and Ripple 2004).

Moving southward from boreal forests of the northern latitudes to southern boreal forests in the northwestern U.S., elevational gradients restrict the extent of boreal forest, resulting in lynx habitat that is naturally more patchy than that closer to the core (Agee 2000, Koehler et al. 2008). Shrub-steppe communities bound lynx habitat at lower elevations, whereas alpine meadows and barren rock restrict it at higher elevations (Koehler et al. 2008). Adding to this, lynx habitat in Washington State is presently fragmented as a result of development, timber harvesting, and fires (Agee 2000, Koehler et al. 2008, Maletzke et al. 2008). Fires have burned over 1,000 km^2 of lynx habitat in Chelan and Okanogan counties since 1985 (Koehler et al. 2008, WDFW 2013). In

2006, the Tripod fire burned most of an extensive area of prime lynx habitat, the Meadows study area used by Koehler et al. (2008).

Lynx are likely to be more sensitive to climate change at the southern range margins not only because these areas are already fragmented but also because these areas represent an extreme on the spectrum of climatic tolerance. Row et al. (2014) found genetic variability of Canada lynx to be well correlated with a winter climatic gradient of increasing snow depth and winter precipitation from west-to-east, and suggest that restricted dispersal across this gradient may be caused by habitat imprinting on snow conditions. Stenseth et al. (2004) found that lynx populations in Canada are structured according to large-scale climatic regimes that influence snow hardness, thought to be directly tied to lynx hunting effectiveness. Broad-scale distribution projections have consistently reported reductions in lynx range, especially at the southern periphery. Gonzalez et al. (2007) found that broad-scale changes in areas that currently receive continuous snow cover for four months and changes in the distribution of boreal forests may shift lynx habitat northward by up to 200 km. Carroll (2007) found that climate change reduced modeled range margin populations in the northern Appalachians by 59%. Finally, Peers et al. (2014), using a model based on bioclimatic data, projected a 29.14% reduction for 2050 and a 50.98% reduction for 2080 within the southern range margin of lynx in North America.

Snow conditions, land cover, horizontal cover, disturbance regimes, canopy cover, and forest openings are landscape features important in lynx habitat selection, and will be affected by climate change. Annual snowfall and snow duration, hardness, and depth are sensitive to temperature and precipitation, and spruce-fir forests, the favored habitat type, are also associated with specific climatic envelopes (Gonzalez et al. 2007, Bayne et al. 2008, Morin and Lechowicz 2008, Higuera et al. 2009, U.S. Fish and Wildlife Service 2014). Feedback systems existing between climate and fire, insect, and pathogen activity are well documented (Higuera et al. 2009, McKenzie et al. 2009, Anderegg and Callaway 2012). Changes in these disturbance regimes will impact land cover, snow conditions, horizontal cover, and the percentage of areas that are forested. Other changes that may influence horizontal cover include growing season precipitation, growing degree days, and the length of the frost-free period (Suchar and Crookston 2010).

Canada Lynx Background and Status

Natural History and Distribution

The Canada lynx is a medium-sized cat found in the boreal and sub-boreal forests of North America (Aubry et al. 2000, U.S. Fish and Wildlife Service 2005). A specialized predator that preys primarily on snowshoe hares, the Canada lynx is able to outcompete other predators such as coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) due to morphological adaptations that allow more efficient foraging in deep, unconsolidated snow (Murray and Boutin 1991, Buskirk et al. 2000b, Interagency Lynx Biology Team 2013). The large padded paws, long hind legs, short black-tipped tail, and long black ear tufts of lynx are a trademark of the species (Bell et al. 2016). Lynx populations in the northern contiguous U.S. represent the U.S. distinct population segment that exists at the southern periphery of the lynx population core in Canada and Alaska (Bell et al. 2016). Washington is one of 14 states that are home to the U.S. population segment, which also includes areas in Colorado, Idaho, Maine, Michigan, Minnesota, Montana, New Hampshire, New York, Oregon, Utah, Vermont, Wisconsin, and Wyoming (U.S. Fish and Wildlife Service 2000, Bell et al. 2016).

The Canada lynx has been listed under the Endangered Species Act as a threatened species in the contiguous U.S. since 2000 (Hoving et al. 2004, Koehler et al. 2008). Although several factors were identified as possible threats to lynx populations in the U.S., the primary reason for the listing is inadequate guidance and regulatory mechanisms for conservation of lynx and lynx habitat on Federal lands (U.S. Fish and Wildlife Service 2000, Interagency Lynx Biology Team 2013). The Washington Department of Fish and Wildlife (WDFW) listed the lynx as a State Threatened Species in 1993 (Stinson 2001).

Preliminary Lynx Recovery Areas were identified in 2005. Based on an examination of historical and recent evidence, the U.S. Fish and Wildlife Service (2005) categorized lynx habitat and occurrence within the contiguous U.S. as fitting into core areas, secondary areas, and peripheral areas. Core areas have strong historical and recent evidence of long-term lynx populations, secondary areas have some historical but no recent evidence of lynx presence, and peripheral areas have sporadic historical records that are not considered sufficient evidence of self-sustaining lynx populations (U.S. Fish and Wildlife Service 2005). Secondary areas are generally thought to have supported self-sustaining populations in the past, but it is unknown whether some still do (U.S. Fish and Wildlife Service 2005).

The WDFW has also designated six Lynx Management Zones (LMZs), or areas of primary lynx habitat where management is expected to be most effective in supporting lynx populations (Stinson 2001). Federal lands make up 92% of these areas (Stinson 2001). These LMZs include the largest zone, the Okanogan LMZ situated within the North Cascades, and in northeastern Washington from west to east, the Vulcan-Tunk, Kettle Range, The Wedge, Little Pend Oreille, and Salmo-Priest LMZs. The LMZs considered most likely to support lynx, based on the order of Stinson's (2001) estimated potential population density, are the Okanogan, Salmo Priest, Kettle Range, and Little Pend Oreille LMZs. Lynx have not been observed in The Wedge and Vulcan-Tunk LMZs after 1990.

A final revised rule for designation of lynx critical habitat was issued on September 12, 2014 that included areas in Maine, Minnesota, the Northern Rockies in Idaho and Montana, the North Cascades in Washington, and the Greater Yellowstone Area of Montana and Wyoming (U.S. Fish and Wildlife Service 2014). The rule designated 4,751 km^2 of habitat as the North Cascades region (Unit 4), which includes portions in both Chelan and Okanogan counties (U.S. Fish and

Wildlife Service 2014). The North Cascades region consists mostly of Okanogan-Wenatchee National Forest lands, but also includes BLM lands in the Spokane district and some Loomis State Forest lands (U.S. Fish and Wildlife Service 2014).

Habitat Associations

General Habitat Associations

Throughout their range, the most commonly found habitat associations for lynx include boreal forest (i.e. spruce-fir, mixed spruce-fir, and lodgepole pine [*Pinus contorta*] types), forest successional stage, understory and overstory or horizontal cover, slope, elevation, aspect, snowshoe hare densities, annual snowfall, snow duration, and snow depth (Koehler 1990a, Murray and Boutin 1991, Slough and Mowat 1996, Buskirk et al. 2000b, Mowat et al. 2000, Hoving et al. 2005, Gonzalez et al. 2007, Koehler et al. 2008, Maletzke et al. 2008, Squires et al. 2010, Vanbianchi 2015).

For annual snowfall, snow duration, and snow depth, there are questions as to the scale and conditions under which selection occurs and why. Studies on lynx distribution in North America have found that annual snowfall and longevity of snow cover are strong predictors of presence (Stenseth et al. 2004, Hoving et al. 2005, Gonzalez et al. 2007, Peers et al. 2014). Conversely, although some local-scale studies suggest snow quality and depth may be important to lynx, several others did not identify snow as a predictor of lynx occurrence. Von Kienast (2003) reported that lynx select for firmer snow when snow remains fluffy throughout the year and Squires et al. (2010) found that lynx in Montana foraged more in deeper snow. However, Hoving et al. (2004) found snowfall to have no significant association with lynx presence at a smaller spatial scale in Maine, as did Walpole et al. (2012) in Ontario. Hornseth et al. (2014) suggested that differences in importance of annual snowfall between models could be attributed to reduced variation of snowfall patterns over their study area, which was smaller (200,000 km^2) than that of the Hoving et al. (2005) and Gonzalez et al. (2007) studies.

Nevertheless, findings on the importance of snow conditions at broader scales are consistent with theory on lynx morphology and ecology. First, as a boreal species, lynx are thought to be adapted to cold, snowy environments (Murray and Boutin 1991, Slough and Mowat 1996) and lynx foot and leg morphology likely translates into competitive advantages in deep, unconsolidated snow (Murray and Boutin 1991, Buskirk et al. 2000b, Interagency Lynx Biology Team 2013). Both lynx and coyotes will select for shallower, firmer snow when it is available, but where their ranges overlap, lynx will shift to deeper, fluffier snow (Murray and Boutin 1991). Peers et al. (2013) found, at a broad scale, that the lynx's higher tolerance to snow cover drove niche divergence from bobcats. Deep, persistent snow is also thought to be needed for snowshoe hares because it provides greater feeding opportunities and effective camouflage for the hare's white winter pelage (Koehler 1990b, Buskirk et al. 2000b, Wirsing and Murray 2002, Interagency Lynx Biology Team 2013, Mills et al. 2013).

Overall, lynx habitat selection is very similar to that of snowshoe hares, their primary prey (O'Donoghue et al. 1998, Squires and Ruggiero 2007). Denser understory, which provides horizontal cover, is characteristic of regenerating forests in the later (15-40 year) part of the stand initiation stage and of multi-layer mature and old-growth stands, forests often demonstrated to be preferred by lynx and snowshoe hares (Aubry et al. 2000, Hodges 2000, Mowat et al. 2000, Hoving et al. 2004, Squires et al. 2010, Interagency Lynx Biology Team 2013). Nevertheless, lynx preference for horizontal cover differs somewhat from that of snowshoe hares. Although snowshoe hares are found primarily in dense horizontal cover (Belovsky 1984, Sievert and Keith

1985, Hodges 2000, Wirsing et al. 2002), there is some evidence that lynx avoid the densest stands. Fuller and Harrison (2010) found foraging lynx in Maine avoided the highest available understory stem structures. Furthermore, although lynx generally avoid large openings within the home range and while hunting (Koehler 1990a, Mowat et al. 2000, Koehler et al. 2008, Maletzke et al. 2008, Squires et al. 2010), they tend to hunt around the edges of forests (Mowat et al. 2000). This suggests that there is an optimal understory density, or combination of within-reach stands with a given understory density, where ease of prey access is balanced with hunting cover. This is referred to by Fuller and Harrison (2010) as the mobility and prey-access hypothesis.

Lynx also prefer spruce-fir overstory (Koehler 1990a, Apps 2000, Vashon et al. 2008, Squires et al. 2010) and avoid deciduous stands (Hoving et al. 2005) and dry forest cover types such as ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menzeisii*) (Squires et al. 2010). Other landscape features consistently demonstrated to be important to lynx are gentle to moderate slope, northerly aspects, human land use such as timber harvest practices, human landscape modification such as road upgrades and snow compaction resulting from recreational activities, and availability of coarse woody debris for denning (Interagency Lynx Biology Team 2013). Across the range of lynx, preference for elevation varies with local conditions, including moisture and temperature patterns (Interagency Lynx Biology Team 2013). In these cases, elevation is a surrogate variable for other ecological processes more directly tied to lynx presence and absence, such as snow conditions, forest moisture, and thus, land cover type and canopy and understory cover.

Washington State Habitat Associations

Studies on lynx local-scale habitat selection in Washington State include Brittell et al. (1989), Koehler (1990a), McKelvey et al. (2000c), Von Kienast (2003), Koehler et al. (2008), Maletzke et al. (2008), and Vanbianchi (2015). Additional detail on these studies and their findings is presented in *Chapter 2*. In general, lynx in Washington State have been consistently shown to select mesic to wet spruce-fir forests, mixed spruce-fir forests, and lodgepole pine at middle elevations (Koehler et al. 2008, Maletzke et al. 2008, Vanbianchi 2015). They avoid dry Douglas-fir and ponderosa pine forests and prefer mild to moderate slopes (McKelvey et al. 2000c, Koehler et al. 2008, Maletzke et al. 2008, Vanbianchi 2015). They also avoid forest openings and recent burns (Vanbianchi 2015). Although understory cover is challenging to include in suitability models, studies that have included it have shown that Washington lynx prefer moderately dense cover (von Kienast 2003, Koehler et al. 2008, Maletzke et al. 2008). These same factors, especially with respect to cover, are correlated with snowshoe hare densities. Koehler et al. (2008) found that lynx prefer elevations between 1,525 m - 1,829 m and this result is generally consistent with other studies that have included elevation (McKelvey et al. 2000c, von Kienast 2003).

Home Range Size, Dispersal, and Exploratory Movements

Although understanding of Canada lynx dispersal behavior is limited, some studies offer insights into behavior and causality. In addition to or sometimes in preparation for dispersal, southern lynx often make exploratory movements, or long-distance forays beyond their established home range, and then return (Aubry et al. 2000). Aubry et al. (2000) suggested that by allowing lynx to locate suitable habitat, these movements may help to improve dispersal success at a later date. Lynx also often disperse in response to the quality of resources available in the home range. Northern lynx dispersal probability is negatively associated with snowshoe hare densities (Ward and Krebs 1985, Slough and Mowat 1996, Steury and Murray 2004) and lynx home range size may increase with decreases in hare densities (Ward and Krebs 1985, Brittell et al. 1989). Home range sizes vary widely across the distribution (Mowat et al. 2000). This variation in movement and habitat selection may suggest that lynx are capable of maximizing net fitness to compensate for landscape fragmentation. Possibly also consistent with this is that Hornseth et al. (2014) found there to be a threshold of habitat fragmentation below which lynx occurrence patterns were not well correlated with habitat amount or fragmentation. This supports the ‘flexibility hypothesis,’ wherein individuals respond to increased habitat disturbance with increased flexibility in habitat selection. However, this does not preclude a threshold of suitability below which lynx are unable to persist. Lynx with especially large home ranges have been known to migrate elsewhere eventually (Brittell et al. 1989).

Travel-habitat selection is less studied. Vanbianchi (2015) found that lynx traveling through lower-quality, matrix habitat in Washington State were more flexible when selecting travel habitat than when selecting core habitat. Though still selecting for >30% canopy cover and avoiding dry forests during travel, lynx appeared more willing to travel through forest openings and recent burns. Squires et al. (2013) used a step-selection function to identify lynx response to landscape heterogeneity in the Northern Rocky Mountains and translated this into a resistance surface. Predictors of use during movements within lynx home ranges included low topographic heterogeneity, higher greenness, and high normalized difference vegetation index (NDVI).

Some landscape characteristics, such as highways, utility corridors, residences, recreation developments, and high topographic relief may redirect, slow, or suspend individual lynx movements to varying degrees (Interagency Lynx Biology Team 2013, Squires et al. 2013), but they are unlikely to prevent movement entirely. Other landscape characteristics, such as fences and large lakes, are more impenetrable (Koehler et al. 2008, Interagency Lynx Biology Team 2013). However, lynx are not considered to be travel-habitat specialists because they are capable of traversing long distances through a variety of landscapes that do not make suitable habitat. Lynx have been observed to cross frozen lakes, desert, farmland, highways, and major rivers during dispersal (Ward and Krebs 1985, Aubry et al. 2000), and dispersal distances of up to 1100 km are known to be possible (Slough and Mowat 1996). There are 15 documented cases of lynx from the northern part of the range dispersing 500 km or more and movements in the northern parts of the range of >100 km are considered characteristic (Mowat et al. 2000). However, it is possible that secondary and peripheral areas of lynx habitat act more or less as stepping stones to facilitate dispersal to and from more core areas (U.S. Fish and Wildlife Service 2005).

Predation Ecology

Lynx fluctuate from being specialists of snowshoe hares in the northern part of their range to being facultative specialists of snowshoe hares in the more southern parts of their range where prey diversity is greater (Roth et al. 2007). Lynx are known to forage opportunistically on red squirrels (*Tamiasciurus hudsonicus*) and other alternative prey, such as Columbian ground squirrels (*Urocitellus columbianus*), when and where available (Aubry et al. 2000, Roth et al. 2007, Squires and Ruggiero 2007), and especially when hare densities are low (Brand et al. 1976, O'Donoghue et al. 1998, Roth et al. 2007). Even so, the general consensus is that high snowshoe hare densities (> 0.5 hares/ha) are needed to sustain lynx (Ward and Krebs 1985, Mowat et al. 2000, Ruggiero et al. 2000, Schwartz et al. 2002). Snowshoe hares are the primary prey of the Canada lynx and make up >50% of the biomass of lynx diets throughout the populations studied in Roth et al. (2007). Snowshoe hares have shown to be essential to lynx survival in Washington State as well. For Washington State, Roth et al. (2007) estimated that snowshoe hares accounted for around 52% of the lynx diet. In north-central Washington, Koehler (1990) reported that red squirrels occurred in only 24% of lynx scats. Also in

Washington Maletzke et al. (2008) observed that 81% (17 of 21) of the prey remains located along lynx trails were snowshoe hare, whereas 14% (3 of 21) were red squirrels.

Objectives

For Canada lynx populations in the Washington-BC transboundary region, the objectives of this project are:

1. To construct reliable transboundary, regional-scale models of core- and travel-habitat suitability that relies on regional-scale habitat-selection drivers and, thereby, minimizes the transmission of associated uncertainties into climate change projections.

2. To identify the most likely projected impacts of climate change on regional pattern, location, quality, and extent of habitat through time.

3. To quantify and demonstrate the range of possible outcomes in projected impacts of climate change on regional pattern, location, quality, and extent of habitat through time and across climate scenarios, with the goal of identifying areas of greatest and least uncertainty.

Objective 1

Problem Statement and Relevance

To model and assess the effects of climate change on Canada lynx and their habitat at a regional scale within the Washington-BC transboundary region, habitat models must be transferrable to future climates. At present, although suitability models for lynx habitat exist, these analyses are based on localized habitat selection at fine to medium resolutions (McKelvey et al. 2000c, von Kienast 2003, Koehler et al. 2008, Maletzke et al. 2008, Vanbianchi 2015). These analyses also used environmental predictors without straightforward analogs in climate projections. Subjective assumptions must be used to translate quantitative relationships from existing models to non-analogous predictors, scales, and resolutions. This is likely to introduce high levels of uncertainty not only with respect to surrogate predictors but also with respect to the scale (i.e. extent and resolution) at which predictors matter.

Analyses

In *Chapter 2*, to obtain a quantitative regional-scale model of lynx habitat suitability, I use lynx Global Positioning System (GPS) collar data collected from the Okanogan-Wenatchee National Forest and Loomis State Forest, in combination with carefully vetted environmental data, to construct cross-validated core- and travel-habitat suitability models for the Washington-BC transboundary region in the program MAXENT (Phillips et al. 2006). I explore the feasibility of expanding these models into British Columbia and examine and compare the importance of predictors to existing studies done at different scales. I use model tuning exercises to ensure appropriate balance between fit and complexity and explore model performance between models using different predictor sets.

Objective 2

Problem Statement and Relevance

Although broad-scale studies on lynx range in North America (Gonzalez et al. 2007, Peers et al. 2014) and regional studies on population impacts (Carroll 2007) under climate futures have been conducted, no studies to date have projected and evaluated lynx habitat at a regional scale for Washington State under future climate scenarios to determine the extent of climate exposure specific to Washington lynx. It is currently unknown whether Washington State can continue to support lynx populations in the future, and if so, to what degree and where. Knowledge of possible and likely outcomes is integral to management for lynx under climate change.

Analyses

This study applies regional-scale habitat suitability models that are specific to the Washington-BC transboundary region to future climate projections to explore these unknowns, and to identify consistencies between models that are indicative of probable outcomes. In *Chapter 3*, I project core-habitat suitability in MAXENT to eighteen different climate futures, characterized by projections of environmental and climate data for three future time periods, two emission pathways or Representative Concentration Scenarios (RCPs), and three Coupled Model Intercomparison Project Phase 5 (CMIP5) models.

I use core-mapping techniques and suitability thresholding to identify habitat cores and range areas throughout the study area, producing associated metrics. I compare aggregated metrics and core maps between time periods and climate scenarios with the goals of quantifying and describing likely changes in pattern, location, quality, and extent of habitat and identifying commonalities and key differences. I use these products to explore the possibility of a shift in the southern range margin of the lynx distribution, identify key core habitats for the future, and assess current and future suitability of habitat presently occupied by lynx. I place an emphasis on changes to presently suitable habitat in Washington State.

Objective 3

Problem Statement and Relevance

Without evaluating the spectrum of possible outcomes under climate futures, assessments of effects on habitat suitability are of limited value. Management is in need of a road map that explores these possibilities, an assessment of the range of possibilities given the future climate spaces that are projected to be possible. Sources of uncertainty within projected future climates include differences in the emission pathways that force global climate models (GCMs), imperfect formulation and complexity of GCMs, and the resulting natural internal variability generated within GCMs (Glick et al. 2011).

Analyses

This study includes multiple Climate Model Intercomparison Project Phase 5 (CMIP5) models at varying ends of the spectrum of climate projections and evaluates the range of uncertainty in the rate and magnitude of climate change effects. In *Chapter 3*, using core habitat and range area metrics, I quantify and depict the range of possible outcomes with respect to regional pattern, location, quality, and extent of habitat through time. I compare aggregated metrics and core maps between time periods and climate scenarios with the goal of quantifying the range of possible outcomes for each time period and scenario and identifying key differences. I also characterize and rank variability between different time periods and climate scenarios using changes in range area. I explore and discuss these results in tandem with those from Objective 2.

CHAPTER 2. HABITAT SUITABILITY MODELS FOR CANADA LYNX IN THE WASHINGTON-BRITISH COLUMBIA TRANSBOUNDARY REGION: A BASELINE FOR PROJECTIONS UNDER CLIMATE CHANGE

Abstract

Although there are already suitability models for Canada lynx (*Lynx canadensis*) in northern Washington, limitations prevent their transfer to projections under future climates. Here, I construct regional-scale models in the program MAXENT than can be applied to future climates without incorporating subjective translation errors. I use spatially rarefied subsamples drawn from lynx Global Positioning System (GPS) collar data from a collaborative study between federal and state agencies to construct core- and travel-habitat suitability models for a study area inclusive of Washington State. I improve on typical applications of MAXENT by conducting tuning exercises and following a model selection process to determine the most suitable model for projecting to present and future climates. Results indicate that habitat selection at a regional scale is different than habitat selection at either local scales or very broad scales. Consistent with previous analyses at all scales and as expected, predictors acting as surrogates for snow longevity, depth, and firmness and environmental conditions that allow productive understory were important. Contrary to expectations, topographic variables such as slope had negligible importance in the core-habitat model, suggesting that regional-scale selection is not as reliant on these drivers as local-scale selection. Predictors that acted as surrogates for vegetation type and snowfall amount were able to be excluded without sacrificing model performance (i.e. other predictors explained selection adequately). This allowed projections to expand north of the

British Columbia border and allowed models to be applied to transboundary outcomes. Suitability was nearly nonexistent within northeastern Washington, including in the Kettle Range, where population status is unknown, suggesting that either habitat selection in northeastern Washington would be fundamentally different or that these areas are no longer suitable. Finally, consistent with previous studies, relationships in the travel-habitat model suggest dispersal plasticity in lynx.

Introduction

To model and assess the effects of climate change on lynx and their habitat at a regional scale within the Washington-British Columbia (BC) transboundary region, habitat models must be transferrable to future climates. Although both core- and travel-habitat suitability models for lynx in northern Washington currently exist, predicting future suitability with them at a regional scale would require many subjective assumptions about selection drivers. Subjective translation of prior analyses is likely to introduce into already uncertain climate futures numerous uncertainties associated with the grain size and scale at which selection drivers are relevant in addition to uncertainties associated with differences in the variables chosen to represent selection drivers. To reduce uncertainty, data for the present day must share the same or similar biases as environmental projections.

Many of the environmental predictors upon which the previous models were based did not have straightforward analogs in climate projections or were defined at resolutions (i.e. grid-cell sizes) that differ from those used in climate projections. Such variables include canopy cover, stream densities, snow firmness, and specific tree-species compositions. Several of these models also included elevation, a variable known to be linked to climatic gradients, which are too complex to be separated. Furthermore, all previous studies in Washington State examined localized lynx habitat selection. Although the study areas used qualify as regions according to spatial ecology, throughout this text, these studies are referred to as local-scale selection studies, because the extent from which available habitat was selected was localized to the lynx use or presence data. In habitat selection studies, the available extent is the geographic extent from which locations are selected to compare environmental conditions at those locations to those at locations where lynx are present. I refer to studies that broaden the area of available habitat for comparison to used habitat as regional-scale selection studies, such as this one, or in the case of studies examining selection across North America, as broad-scale selection studies.

Previous Habitat-Selection and Suitability Models for Canada Lynx

Habitat Selection in Washington State

Previous studies of lynx habitat selection in Washington State, including methods, scale, available extent, resolution, study area, and important predictors are summarized in **Table 2.1**. In a reanalysis of data collected from 1981 to 1988 for two previous studies (Brittell et al. 1989, Koehler 1990a), McKelvey et al. (2000c) evaluated Canada lynx (hereafter "lynx") habitat selection for vegetation types, stream densities, road densities, elevation, slope, and aspect on the Okanogan National Forest in Washington. McKelvey et al. (2000c) found that lynx in north central Washington preferred areas at elevations between 1,400 m and 2,150 m. Within this band, lynx selected slopes less than 10%, moderate stream densities, and lodgepole pine (*Pinus contorta*) cover in winter. Lynx avoided Douglas-fir (*Pseudotsuga menziesii*) cover types and selected northeast aspects during the summer. McKelvey et al. (2000c) found little evidence that lynx either prefer or avoid roads.

Von Kienast (2003) evaluated lynx habitat selection on the Okanogan Plateau in the north-central Cascade Range, comparing forest conditions on lynx travel routes to those on systematically arrayed availability transects during the winters of 2000/2001 and 2001/2002. The study found that lynx habitat selection at this scale was tied to elevation, slope, understory cover, densities of tree-size classes, snow firmness (as judged by sinking depth), and snowshoe hare (*Lepus americanus*) abundance as variables.

Koehler et al. (2008) used snow-tracking data and pre-fire landscape conditions from northern Washington in a univariate analysis to identify key factors in lynx habitat selection. They found that during winter in the Black Pine Basin of the Okanogan-Wenatchee National Forest in northern Washington, lynx preferred Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) forests, moderate canopy and understory cover (11-39%), and elevations between 1,525 m - 1,829 m. Lynx avoided Douglas-fir and ponderosa pine (*Pinus ponderosa*) forests, forest openings, recent burns, open canopy and understory cover, and steep slopes (>30°). Koehler et al. (2008) then modeled suitable winter lynx habitat in Washington State based on a logistic regression model including those factors. Maletzke et al. (2008) used these data in combination with prey carcass and snowshoe hare abundance data to determine the factors most associated with lynx hunting behavior and predation, and used the sinuosity of hunting trails as an index of hunting habitat suitability.

Most recently, based on the same Global Positioning System (GPS) collar data used in this analysis (see *Occurrence Data*), Vanbianchi (2015) used random-forest models to evaluate remaining post-fire lynx core hunting, resting, and denning habitat, in addition to travel habitat in Washington State. Vanbianchi (2015) found that lynx core- and travel-habitat selection within the study area was driven predominantly by medium-resolution (810 m grid-cell size) selection patterns. At this resolution, for core habitat, lynx preferred Engelmann spruce, subalpine fir, lodgepole pine, and mixed sub-boreal Douglas-fir forests. They also selected for higher growing season precipitation, areas with greater moisture accumulations found in drainages as measured by Compound Topographic Index, and for cooler, moister, northeast-facing slopes as measured by Heat Load Index, while avoiding dry forests, forest openings, steep slopes, and recent burns. Lynx travel-habitat selection was more flexible than core-habitat selection. Lynx used a wider array of habitat types. Though still selecting for >30% canopy cover and avoiding dry forests during travel, lynx traveled through open areas and recent burns with greater frequency, making use of cover within these areas, such as fire skips.

These previous studies in the North Cascades were all conducted at fine to medium resolutions (est. 90 m - 2 km), regional scales (est. roughly 20 km^2 to 1,700 km^2 study areas), and used an available extent around lynx use or presence data defined as the area surrounding most or all of the data (i.e. the immediate vicinity). Some employed a buffer around the data of roughly 766 m (Vanbianchi 2015) or up to 4.8 km (McKelvey et al. 2000c). As such, though similar in resolution to this study, these methods primarily identify habitat selection at a local scale (i.e. local available extent) within the Okanogan region. My analysis seeks to identify regional-scale patterns in habitat selection that can be used to delineate suitable from unsuitable habitat within a much greater regional extent (i.e. the Washington-BC transboundary region vs. the North Cascades).

Table 2.1: Summary of previous habitat selection studies in Washington State

	McKelvey et al. (2000)	Von Kienast (2003)	Koehler et al. (2008)	Vanbianchi (2015)
Methods	Various including logistic regression	Logistic regression; use vs. availability trails/transects	Univariate analysis and logistic regression; use vs. availability trails/transects	Random-forest models
Study Area Evaluated *	Regional: Home range area up to study area (1,666.2 km^2)	Regional: 200 km^2 study area	Regional: 211 km^2 study area	Regional: 250 km^2 study area and 1,225 km^2 study area
Available Extent **	Local: Up to 4.8 km presence buffer	Local: Study area	Local: Study area	Local: ~766 m presence buffer
Resolution ***	Unspecified	Medium: Est. 2 km	Fine: Est. 460 m	Fine: 90 m Medium: 810 m
Study Area	Okanogan NF	Okanogan Plateau in the north-central Cascade Range	Black Pine Basin: Okanogan-Wenatchee NF	North Cascades: Black Pine Basin and the Loomis study area
Predictors	Elevation, slope, vegetation type, aspect, and stream density	Elevation, slope, understory cover, tree size class and density, snow firmness, and snowshoe hare abundance	Elevation, slope, vegetation type, canopy and understory cover, and recent burns	Slope, vegetation type, canopy cover, moisture (growing season precipitation, CTI, heat load index), distance to high severity recent burns

* A *regional* study area is defined, for the purpose of this analysis, as an area between 1 km^2 - 10,000 km^2.

** Available extent refers to the available area to which lynx habitat use was compared. In this study, l*ocal* refers to an available area mainly confined to the immediate vicinity of the lynx presence or use data. *Regional* refers to an available area extended from the presence data by a distance equivalent to the average dispersal distance of the species.

*** *Fine resolution* is defined as 1 m - 0.99 km, whereas *medium resolution* is defined as 1 km - 100 km. In some cases, resolution was not specified and was estimated based on the methods used in the study.

Broad-Scale Habitat Suitability and Distribution in North America

Continental-scale studies have found that snowfall and longevity play a role in lynx habitat selection. For Hoving et al. (2005), a broad-scale (512,000 km^2 study area), 100-km-resolution model for eastern North America including 10-year mean annual snowfall and avoidance of deciduous forest best predicted lynx occurrence with a 94% accuracy. The model containing only snowfall correctly predicted 92% of the verification points, and Hoving et al. (2005) speculated that snowfall and lack of deciduous forest may act as proxies for prey density. Similarly, using an 8-km resolution, Gonzalez et al. (2007) found that lynx in the U.S. require four months of continuous snow cover from December through March and a high probability of snow in January.

More recently, Peers et al. (2013) used MAXENT species distribution modeling software to model and compare the environmental and climatic niche over the southern range of lynx in North America at a cell size of 10 km for the present day. They found, at a broad scale, that the lynx's higher tolerance to snow cover drove niche divergence from bobcats (*Lynx rufus*). Mean temperature of the warmest month, snow depth, and ecoregion had the highest standalone variable importance.

Objectives and Expectations

My overall objective for this analysis was to construct both core- and travel-habitat suitability models for Washington State and the surrounding area (the Washington-BC transboundary region) that would project more reliably onto future climates. A secondary objective was to compare my modeling outcomes to previous habitat-selection analyses to identify differences in core- and travel-habitat selection between differently scaled models. Using lynx Global Positioning System (GPS) collar data from a collaborative study between federal and state agencies, I applied statistical modeling in MAXENT (Phillips et al. 2006) to environmental data acting as surrogates for drivers of lynx habitat selection to construct habitat suitability models at a regional scale. MAXENT is an extensively used program that relies on presence-only occurrence data combined with background feature data to model species distributions based on the maximum entropy principle (Jaynes 1982).

I compared models that used a set of screened predictors thought most proximal to lynx habitat selection drivers to those that used an expanded set of climatic predictors. I also assessed the effect of dropping predictors that constrained the geographic extent of projections to south of the Washington-BC border on model performance. I expected that climatic variables provided to the models might be capable of capturing habitat selection relationships in the absence of these geographically constraining predictors. For these differing predictor sets, I improved on typical applications of MAXENT models by first conducting tuning exercises and then following a model selection process to determine the most suitable model for projecting to present and future climates. I then evaluated and compared predictor importance in the final models.

Based on previous habitat-selection analyses, I expected that relationships would be stronger in the core-habitat model than in the travel-habitat model, but that lynx core- and travel-habitat selection at a regional scale in the study area would be tied to the primary drivers slope, aspect, road proximity, potential vegetation type, annual snowfall, snow duration, snow depth, and horizontal cover. Although I expected that habitat-selection drivers identified in previous studies would play a large role in habitat selection at a regional scale, I expected to see some differences not only in the importance of specific drivers but also in their relative quantitative roles in habitat selection.

Materials and Methods

Statistical Modeling

Thermodynamic theories support the application of MAXENT to species distributions (Phillips et al. 2006). The second law of thermodynamics states that in a closed system, lacking external inputs, entropy always increases (Harte 2011). Thus, MAXENT applications assume that species distributions will tend toward geographic distributions consistent with maximum information entropy, realized as a least-biased estimate subject to constraints supplied by the modeler (Phillips et al. 2004). The default outputs from the MAXENT software are probability of suitability over all grid cells in the projection area and associated metrics of model fit, including a predictor jackknife. These default outputs can be based on test data only or on training data as well, depending on whether training data is supplied to the model.

MAXENT software became available in 2004 and has been shown to outperform other algorithms used to develop species distribution models based on presence-only data (Elith et al. 2011). As such, MAXENT is appropriate for evaluating projections of habitat suitability at regional scales. The program uses environmental data, both categorical and continuous, to define the features, an expanded set of the transformations of the original covariates (Elith et al. 2011). To assess predictor importance, the MAXENT software can be made to compute a predictor jackknife that quantifies the information explained by each predictor when used in isolation and the information lost when only that predictor is excluded.

MAXENT prevents overfitting through the use of an approach called L1-regularization, wherein the coefficients of predictors are weighted (penalized) to balance model fit against complexity (Phillips et al. 2006, Elith et al. 2011). The L1-regularization also makes MAXENT more stable with respect to collinearity in predictor variables because the regularization shrinks some feature coefficients (often collinear with others) to zero (Elith et al. 2011). Although MAXENT already includes this penalty in the form of a regularization parameter for each feature class (Phillips et al. 2006), overfitting should still be addressed on a case-by-case basis because the regularization parameters can have widely varying effects due to the specific environmental and observation data and feature classes used in the model (Elith et al. 2011, Radosavljevic and Anderson 2014). The algorithm can incorporate many predictor variables (Phillips et al. 2004), but it is still wise to screen candidate variables, especially when the model outcomes will be used to project habitat in a different region or climate (Elith et al. 2011).

MAXENT provides the area under the receiver operating characteristic (ROC) curve (AUC) as a measure of the model's discriminatory ability, but AUC should be interpreted only in a relative sense for these presence-only models. If background extent is much larger than the area of the training data, AUC can be inflated (Lobo et al. 2008, Edrén et al. 2010, Radosavljevic and Anderson 2014) because AUC is sensitive to the manner in which pseudo-absences are selected (Lobo et al. 2008, Edrén et al. 2010). This is because MAXENT uses fractional predicted area in lieu of commission error in plotting the ROC curve. Consequently, AUC is not comparable between differing background extents (Lobo et al. 2008, Wisz et al. 2008, Edrén et al. 2010), nor should it be interpreted as an absolute measure of fit *sensu* Swets (1988) or as an accurate measure of whether a model is overly complex (Radosavljevic and Anderson 2014).

Also as a measure of fit, MAXENT plots omission rate against cumulative threshold. Omission rate is the percentage of the test samples that are located within grid cells not predicted to be suitable after application of a threshold (Phillips et al. 2006). This measure of fit is based on the cumulative outputs derived in MAXENT; MAXENT's raw probability outputs are transformed relative to the range of probabilities in the map, and thus to the expected omission rate, to generate the cumulative output (Phillips et al. 2006, Phillips and Dudík 2008, Philips 2010). As such, a binary model obtained by setting a cumulative threshold equal to *t* will have a predicted omission rate equal to *t* (Phillips et al. 2006, Phillips and Dudík 2008, Philips 2010). In the omission rate plots produced in MAXENT, a good model will have a test omission rate at a given cumulative threshold that is close to the predicted omission rate. Omission rates lower than this indicate that the model is predicting higher suitability in areas where it is not necessarily there and omission rates higher than this indicate that the model is failing to predict suitability in areas where it is likely there.

Dealing with geographical sampling biases prior to modeling with MAXENT is critical. Models based on observation data that include biases due to sampling effort limitations can bias selection results toward features that facilitate access, such as distance to road (Phillips 2009). By default, MAXENT selects background sample (or pseudo-absence) locations from the full spatial extent of the environmental data provided to the software. If that extent is defined in a manner that does not consider sampling bias, the biases will be reflected in the outcome. The landscape used for the background sample should exclude unsearched areas where occurrence is likely (Elith et al. 2011). Options for accounting for sampling bias include application of a bias grid scaled to represent survey effort across the landscape (Elith et al. 2006) or a mask over geographical areas where absence cannot be assumed (Radosavljevic and Anderson 2014).

MAXENT predictions are highly sensitive to the choice of background extent (Elith et al. 2011). The size of the geographic area from which the background sample points are selected is important in striking a balance between discriminatory ability and the amount of extrapolation required when projecting suitability in different environments or climates. A broader background will mean less extrapolation when applied to a novel environment, but less specificity in distinguishing between levels of habitat suitability (Elith et al. 2011). Directional biases can occur if the background sample is selected from an extent that is directionally shifted in geographic space with respect to the core of the presence localities (Elith et al. 2010, 2011).

The MAXENT software incorporates several tools for exploring how environmental novelty impacts predictions in new environments (MESS Maps and model "clamping") and their use is described in the supplemental materials for Elith et al. (2010). Multivariate environmental similarity surface (MESS) maps depict differences between the environment used to train each model and the environment to which the model is projected by measuring the similarity of each grid cell to the reference grid cells used in the analysis (Elith et al. 2011). Negative values indicate that at least one predictor has a value that is outside the range of the training space predictors, whereas positive values indicate similarity to the feature values used in the model, with a score of 100 meaning that values are all exactly equal to the median values found in the training space predictors (Elith et al. 2010). Clamping constrains features to within the range of the training data, but clearly would influence projections for which major changes in features would necessitate extrapolation outside of training data.

Occurrence Data

The presence locations used to model habitat suitability were derived from GPS telemetry data acquired through a collaboration between the Washington Department of Fish and Wildlife (WDFW), Washington Department of Natural Resources, U.S. Forest Service, U.S. Bureau of Land Management, and the U.S. Fish and Wildlife Service (**Figure 2.1**). Animals were trapped using box traps and collared between January 2007 and April 2012. These animals include twelve individuals, one female and eleven males, in the Loomis State Forest and five, two females and three males, in the Black Pine Basin (Vanbianchi 2015). All GPS collars were programmed to attempt a fix every 4 hours, except one collar that was programmed to acquire a fix every 6 hours. Length of monitoring varied between several months to several years for each lynx. Only males made exploratory movements or dispersed. During the study, four lynx explored greater than 35 km outside of their homes range and two of these lynx eventually returned.

To prepare the GPS telemetry data for modeling core habitat, I first applied several filters to scrub the data for duplicates, errors, and imprecise locations. Locations recorded when the collar was no longer on the animal, fixes that failed to acquire coordinates, periods of apparent collar malfunction as judged by consistently low fix rates, and locations that would have required a physically impossible speed were removed. I used a movement speed filter in the R Package *trip* version 1.1-21 (Sumner 2015) with a threshold of 1.46 km/hr based on a literature review of possible lynx movement speeds (Slough and Mowat 1996, O'Donoghue et al. 1998). Positions with low accuracy fixes, 2D fixes with a dilution of precision (DOP) > 10 and any fixes with a DOP > 20 were also removed (Ganskopp and Johnson 2007).

Next, I applied several filters to minimize bias. To remove the influence of the release location, I removed any observations that were within 30 m of trap locations and/or acquired less than 2 days following collaring (Edrén et al. 2010). I also removed extraterritorial movements > 35 km from home ranges to eliminate landscape use patterns for dispersing lynx from the analysis, as short exploratory movements outside and back to the home range are still likely representative of core-habitat selection. For the same reason, transient lynx that demonstrated no consistent home range pattern were also removed from the dataset (Vashon et al. 2008). This included only one male lynx with no definable home range. All observations were re-projected from the WGS84 geographic coordinate system (GCS) to the North America Albers Equal Area Conic projected coordinate system (PCS) to match the environmental predictors (see *Environmental Data*). Following preparation, 17,842 points were available for analysis from 14 individuals, three of which were female and all of which were adults.

I used Monte Carlo methods in RStudio (R Core Team 2013, RStudio Team 2015) with the help of the R packages *sp* (Pebesma and Bivand 2005, Bivand et al. 2013) to resample the full resulting dataset randomly (n = 17,842), producing 200 spatially rarefied subsamples (Edrén et al. 2010, Kassara et al. 2014). GPS telemetry data were highly clustered within the two collection areas. Spatial autocorrelation within presence records can inflate estimates of performance and increase overfitting (Radosavljevic and Anderson 2014). To address this issue, I separated the observations into lynx seasons and drew one point at random from each lynx within each season where data were available, for a total of 53 observations per subsample. For the fall season, observations were not available for one of the 14 individuals retained in the dataset. For winter, observations were unavailable for two individuals. Subsample replicates were drawn at random with the requirement that all were at least 1 km apart.

For the travel-habitat model, I used the scrubbed data but with the exception that I did not remove extraterritorial movements or transient lynx observations but instead manually removed clustered observations that denoted little movement and movements within observable home ranges. Four individuals were available for sampling in this case. Clustered movements were defined as more than 10 subsequent observations within an area of 16 km^2 or less over a period of 3 days or more and were assessed by estimation on a cluster by cluster basis until no such clusters remained. I again used random resampling on the resulting dataset (n = 368), producing 10 spatially rarefied (i.e. with minimum separation of 1 km) subsamples for modeling, each containing 40 presence locations. I did not attempt to partition the data by season as with the core-habitat subsamples. Two examples of how telemetry data were partitioned are provided in **Figure 2.2**.

Environmental Data

I prepared environmental data describing possible predictors of lynx habitat for which climate projection analogs also exist, selecting only predictors with future climate projections available for Coupled Model Intercomparison Project 5 (CMIP5) models for the Representative Concentration Pathways (RCPs) 4.5 and 8.5 (i.e. emission pathways). Predictors used were mostly thirty-year measures of central tendency or range of the relevant variables with the exception of slope, aspect, and distance to road types. There was some degree of offset in the exact thirty-year period used due to differences in data availability, but in general, data were selected that best exemplified the landscape at the time that the GPS telemetry data were collected. A list of all predictors used in the models is provided in *Appendix A*, along with a designation of the type of predictor (categorical vs. continuous), the abbreviation, and the time frame over which the measures were summarized.

To test cautions provided by Elith et al. (2011) that not prescreening predictors can increase the uncertainty associated with extrapolation outside the range of predictors, I partitioned predictors according to two fundamental conceptualizations of regional-scale lynx habitat selection. The *full* predictor set assumed that little is known about the drivers of regional-scale lynx habitat selection and employed all predictors in *Appendix A*, including all seventy-nine 30-year average yearly and seasonal ClimateWNA Climate Normals (1981-2010) (Wang et al. 2012). Models using this predictor set were produced with the knowledge that MAXENT penalizes features offering little additional contribution to model gain, a goodness of fit measure. The *proximal* predictor set assumed that previous research has already identified the major drivers of regional-scale lynx habitat selection and included a subset of predictors listed in *Appendix A* most proximal to these drivers. For this set, I used literature review and pre-selection to identify predictors related to established drivers, grouped predictors according to their expected relationship with identified habitat-selection drivers (e.g. April 1 snow water equivalent was grouped into the snow quality category), and subsequently removed less-proximal surrogates from each grouping.

For the proximal predictor set, from the known or frequently identified drivers of lynx habitat selection, I selected slope, aspect, vegetation type, annual snowfall, snow duration, snow depth, road proximity, and horizontal cover as primary drivers. I used either explicit or implicit proxies for these variables as predictors. Evidence of road avoidance or preference is mixed, so I included distances to primary, secondary, and local roads as predictors, developing the layers using 2014 TIGER/Lines (U.S. Census Bureau 2014) and Digital Road Atlas (DRA) Master Partially-Attributed Roads from the GeoBC data catalogue. Slope and aspect were derived from the 1 arc-second USGS National Elevation Dataset (NED). Slope and aspect were selected because, in previous habitat-selection analyses, lynx have been found to avoid hotter aspects, especially during summer (McKelvey et al. 2000c, Vanbianchi 2015), and steeper slopes (McKelvey et al. 2000c, von Kienast 2003, Koehler et al. 2008, Maletzke et al. 2008, Vanbianchi 2015).

Previous studies have shown that lynx in the study area select for Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), and mixed sub-boreal Douglas-fir (*Pseudotsuga menziesii*) forests (Koehler et al. 2008, Maletzke et al. 2008, Vanbianchi 2015). More generally, lynx are known to prefer subalpine forest, while also occasionally using mixing zones. To capture vegetation type as a predictor, I used MC2 potential vegetation type projections from the Integrated Scenarios of the Future Northwest Environment Project as a baseline (Sheehan et al. 2015). These projections used a vegetation classification applicable to demonstrated habitat selection, including subalpine and temperate evergreen needleleaf forests. These types are inclusive of subalpine fir, Engelmann spruce, and lodgepole pine occasionally mixed with Douglas fir and ponderosa pine. The MC2 dynamic global vegetation model (DGVM) includes three modules: biogeography, biogeochemistry, and fire disturbance and simulates vegetation types, carbon fluxes, nitrogen and water, and wildfire (Lenihan et al. 1998, Bachelet et al. 2001). Simulations are available both with and without fire suppression efforts beginning in 1950. Outside of this, simulation of potential vegetation assumes no direct human intervention.

To assemble modal 1981-2010 MC2 potential vegetation type over the study area, I used yearly MC2 vegetation type raster outputs produced based on upscaled historical Parameter-elevation Regressions on Independent Slopes Model (PRISM) data (Daly et al. 2008, Sheehan et al. 2015) from 1895-2010. I used outputs from models that incorporated fire suppression dynamics. Although differences exist between potential and actual vegetation types within the study area, using potential vegetation types is advantageous because doing so eliminates uncertainties associated with differences in non-climatic drivers of present-day conditions vs. future projections. To ensure the best possible match between the MC2 model outputs and reference datasets, Sheehan et al. (2015) calibrated MC2 outputs using Kuchler's (1975) potential vegetation map, Leenhouts' (1998) potential fire return intervals matched to Kuchler’s vegetation types, and the National Biomass and Carbon Dataset (NBCD) (Kellndorfer et al. 2012). There was a 47% full match and a 33% minimal mismatch between the MC2 results and Kuchler's (1975) potential vegetation (Sheehan et al. 2015).

Lynx have been shown to rely on sufficient cover for hunting. There is no comprehensive understory or horizontal cover dataset for the study area in question. In a study to identify proxies for understory cover and potential understory biomass indices, Suchar and Crookston (2010) found elevation and slope as well as certain climate variables to be reasonable predictors of understory cover and biomass indices. Nevertheless, it is important to note that actual understory cover responds to both macro- and micro-scale conditions that can be exceptionally difficult to capture in a model (Suchar and Crookston 2010), including fire history, vegetation type, climate, and microclimate. Despite this, for lack of a more direct method, I deemed substitution of proximal variables to be the most suitable and realistic solution for accounting for potential cover dynamics.

Consistent with the results of Suchar and Crookston (2010), I selected 30-year variables from ClimateWNA most similar to those with highest significance in models of shrub cover. Variables included mean temperature of the warmest month, degree-days above 5°C (growing degree-days), mean annual summer (May to Sept.) precipitation, and frost-free period. I also supplemented this with Hargreaves Climatic Moisture Deficit and compound topographic index (Vanbianchi 2015) as wetness indices. Mean annual temperature was dropped from the proximal predictor set due to high collinearity with both degree-days above 5°C and frost-free period (Spearman’s rho > 0.94) and because it is a distributed annual variable that may dampen modeled responses as a result of its inverse relationship with both understory growth during the growing season and snow qualities during the snow season. Other collinearities were observed between included predictors. However, no additional predictors were eliminated because of

MAXENT's inherent stability with respect to collinearity. In addition to climate variables, I included a measure of 30-year maximum burn severity, extracting maximum burn severity for each grid cell from 1984-2013 National Monitoring Trends and Burn Severity (MTBS) Burn Severity Mosaics (Eidenshink et al. 2007).

Many studies have shown that snow amount, longevity, and firmness are important to lynx habitat selection at multiple scales (Murray and Boutin 1991, von Kienast 2003, Hoving et al. 2005, Gonzalez et al. 2007, Squires et al. 2010, Peers et al. 2013). As proxies for amount, longevity and quality of snowpack, I added degree-days below 0°C from ClimateWNA and April 1 snow water equivalent (SWE). Degree-days below 0°C reflects on the ability of snow to remain frozen or to thaw, potentially forming a hard freeze-thaw crust if refreezing occurs. Thirty-year mean (1976-2005) April 1 SWE was adapted from Variable Infiltration Capacity (VIC) model (Liang et al. 1994) outputs also from the Integrated Scenarios Project. April 1 SWE is a measure of the amount of water contained within the snowpack. Amount of snowfall combined with degree-days below 0°C is likely also a reasonable proxy for snow depth and longevity. It should be noted that variables selected as proxies for understory growth potential are also likely related to the longevity of snowpack, including degree-days above 5°C and frost-free period.

I prepared all spatial layers at a grid-cell size of 1 km in the North America Albers Equal Area Conic PCS. Additional information on GIS preparation of the spatial predictors is described in *Appendix B*. Most predictors were available at an extent that covered the entirety of the study area depicted in **Figure 2.1**. However, three predictors (modal MC2 potential vegetation type, 30-year maximum burn severity, and April 1 SWE) were limited in extent and excluded most or all of the British Columbia (BC) portion of the study area (**Figure 2.3**).

Modeling Methods

Settings

In all models, I used default MAXENT software settings with several exceptions. MAXENT uses five feature classes: linear, product, quadratic, hinge, and threshold. Although threshold and hinge features allow MAXENT to fit more complex relationships, these relationships are often difficult to interpret (Edrén et al. 2010). To enforce smoother response curves and make interpretations more straightforward, I turned off threshold and hinge features, leaving only linear, quadratic, and product features for all models. Clamping of response curves to within the range of the predictor values was turned off for all projections, as clamping during exploratory modeling had unpredictable effects on projections and produced projections that were unquestionably poor in areas where extrapolation was necessary. MESS analysis was performed for all models. MAXENT's default logistic output was used to define relative probability of suitability across the study area, with the assumption that habitat selection is equivalent to habitat suitability. The modeling process is described below as well as outlined in **Figure 2.4**.

Background Extent

To achieve a balance between specificity and extrapolation, I used an extent defined as a 100-km buffer around all observation points. This background extent corresponds to a region consistent with estimates of median and average long-distance lynx dispersal in the northern part of their range (Poole 1997, Mowat et al. 2000). In selecting a background extent for MAXENT modeling, it is advisable not to include areas where absence may in part be due to dispersal limitations (Elith et al. 2011, Radosavljevic and Anderson 2014). Peripheral lynx in the Northern Cascades are known to have high immigration from BC populations (McKelvey et al. 2000a, 2000b). However, evidence of self-sustaining lynx populations south of critical habitat in the Northern

Cascades is nonexistent. This may be a result of lack of detection or of absence. In the latter case, absence may have resulted from a combination of limited connectivity and lack of suitability. To avoid any chance of conflating the two potentialities, these more distant areas where accessibility cannot be assured were excluded from the background sample extent. A 100-km buffer is also consistent with advice that the study area capture the entire area of the process in question, with a buffer to allow for calculation of spatial statistics and inferences (Fortin and Dale 2005).

For animals that establish regional and often adjacent territory, such as lynx (Burdett et al. 2007, Vashon et al. 2008), the collection of GPS telemetry data from opportunistic capture and collaring efforts presents a unique form of geographic bias because of the possibility of omitting neighboring animals from the sample. Masking unsampled but potentially suitable areas from the background extent has been shown to produce models that generalize better to independent test datasets, are more realistic, and have higher discriminatory power (Radosavljevic and Anderson 2014).

For the core-habitat model, I clipped an area representative of suitable but unsampled lynx habitat from the 100-km buffer background extent. I used WDFW Lynx Management Zones (LMZs), which represent areas of suitable lynx habitat in Washington State (Stinson 2001), to mask out suitable habitat with the exception of a 5-km buffer drawn around the lynx presence points. For lack of knowledge of specific suitable areas within BC, I then constricted the available background extent to the northern border of Washington State, excepting the 5-km observation buffer. The result was the final background extent (**Figure 2.5a**), used as a baseline for background extents in all MAXENT models of core habitat. This extent was provided to

MAXENT as a binary mask, where values of one indicate areas that should be used for selection of available background points and absence of values indicate areas that should not.

To facilitate comparison of model performance between certain models, I also derived a background extent (**Figure 2.5b**) from the intersection of the original background extent (**Figure 2.5a**) with the areas that the constraining predictors shared (**Figure 2.3**). The background extent used for the travel-habitat models was a minimum convex polygon around the exploratory observation dataset extended with a 5 km buffer (**Figure 2.5c**).

Projection Area

The area to which the trained MAXENT models were projected was either (a) the entire study area (**Figures 2.7** and **2.9**), or (b) the entire study area constrained by the predictors most limited in extent (**Figures 2.8** and **2.10**), depending on the predictor set used to train each of the models. This is because MAXENT automatically limits the projection area to the grid cells shared between all predictors included in the model.

Model Tuning and Selection

Model Tuning

The observation data used in this analysis were clustered by comparison with the background extent, the predictor sets were large, and the background extents were large. As such, the modeling approaches compared in this study involved differing, though high, degrees of model complexity. The potential for overfitting increases with model complexity and preliminary modeling indicated overfitting was likely to be a problem. Given this, prior to model selection, I conducted a regularization parameter tuning exercise on all model types to determine the optimal regularization level. To control for model complexity, MAXENT allows the user to adjust a regularization multiplier, set at a value of 1 by default, that is applied to the regularization parameter for each feature class (Radosavljevic and Anderson 2014). This parameter weights the feature class coefficients to balance model fit and complexity. To find the appropriate multiplier, I partitioned subsamples into training and testing datasets using the *k*-fold cross-validation procedures built in to the MAXENT software and ran models that varied the amount of regularization, using similar methods as those employed by Radosavljevic and Anderson (2014). In the absence of a sufficiently sized independent test dataset, this method was useful to this study in that it provided an indication of how well models generalized to the portions of the data that were omitted.

To tune the core-habitat models, eleven models were run in MAXENT for each model type, each using one subsample (n = 53) with 10-fold cross-validation (Radosavljevic and Anderson 2014). Each of the eleven models used a different regularization multiplier, ranging from 0.25 to 20, to calibrate the model. These methods were similar to Radosavljevic and Anderson (2014), with the exception that I expanded the range of regularization multiplier values when thresholds in model-fit metrics were not initially identifiable below a regularization multiplier value of 10 for all models. A similar approach was used to tune the travel-habitat models, with nine models run using regularization multipliers ranging from 0.25 to 2.

Predictor Sets

As previously discussed, for core-habitat modeling, I formed two different predictor sets representing different conceptualizations of drivers that may influence regional-scale lynx habitat selection (i.e. the *full* and *proximal* predictor sets) to test for differences in model performance. I subjected each of these predictor sets to a secondary split, producing a grand total of four predictor sets. Using the three predictors (vegetation type, April 1 SWE, and 30-year maximum burn severity) where data were not available for the entire study area to project habitat suitability would have constrained all projections to south of the Washington-BC border and eliminated the applicability of the analysis to transboundary questions. As one of the goals of this analysis was to identify whether projections of habitat suitability could be expanded north of the BC border, to explore the effect of these predictors on both the *full* and *proximal* model performance, I ran additional models that dropped these predictors.

Models that dropped these predictors would have had naturally dissimilar background extents to those that did not. Hence, to allow comparison, I ran the dropped predictor models both with and without a background extent (**Figure 2.5b**) derived from the intersection of the original background extent (**Figure 2.5a**) with the areas that the constraining predictors shared (**Figure 2.3**).

Model Evaluation

Computations, Plots, and Maps

Computation of average model-fit metrics, AUC, predictor jackknifes, habitat suitability, and MESS maps was done in RStudio using MAXENT outputs, with the last two computations requiring the help of the R package *raster* (R Core Team 2013, RStudio Team 2015, Hijmans 2016). All plots of model-fit metrics and all predictor jackknife plots were produced in RStudio using the packages *Cairo* (Urbanek and Horner 2015), *scales* (Wickham 2016), and *ggplot2* (Wickham 2009). Maps were produced in ArcGIS 10.3 (ESRI 2014). Omission rate plots were generated by MAXENT.

Core-Habitat Model Types

Modeling goals resulted in six variations in core-habitat modeling approaches to which tuning exercises and model selection were applied. Three decision points affected the total number of model types tested: use of full vs. proximal predictor sets, dropping vs. including the three constraining predictors, and use of a full vs. a constrained background extent (**Figure 2.5a, b**). **Table 2.2** summarizes the resulting approaches and provides reference model type numbers. Note that models that included the constraining predictors could only be run with the constrained background extent because MAXENT can only use grid cells from the background extent where all predictors have a value.

Table 2.2. Model types and associated modeling approaches used in this analysis

Model Type Number	Predictor Set*	Background Extent	Constraining Predictors
1	Full	Full	Dropped
2	Full	Constrained	Dropped
3	Full	Constrained	Not Dropped
4	Proximal	Full	Dropped
5	Proximal	Constrained	Dropped
6	Proximal	Constrained	Not Dropped

* *Full* refers to the full predictor set including the expanded set of climatic variables and *proximal* refers to the proximal predictor set of preselected predictors. Model type numbers are used for reference throughout the text.

Evaluation of Tuning Exercises

I averaged the model-fit metrics and suitability projections generated by MAXENT across the 10 iterations of cross-validation for each multiplier used (Radosavljevic and Anderson 2014). For each of the regularization multipliers tested within each of the model types, I assessed performance using the methods of Radosavljevic and Anderson (2014). I quantified overfitting using two threshold-dependent measures, one threshold-independent measure, and through visual examination of the projections. These measures were derived from model-fit metrics produced using the 10-fold cross-validation.

For the threshold-independent measure, I quantified overfitting as the magnitude of difference between the training AUC and the test AUC. The two threshold-dependent measures were test data omission rate at the lowest presence threshold and at the 10th percentile presence threshold of the training data. Thresholding rules apply to the values used to construct binary suitability surfaces, where grid cells are considered suitable only above that threshold. The lowest presence threshold is the lowest prediction value containing a training observation, and the 10th percentile presence threshold is the value that excludes 10% of the training observations. Deviations from expected omission rate (zero at the lowest presence threshold and 10% at the 10th percentile presence threshold) were used to quantify overfitting.

I considered the three measures simultaneously to select the optimal regularization multiplier for each of the model types. Multipliers were selected based on the earliest point at which the trend for all three measures of fit approached a horizontal line. I also visually compared projections across different regularization multipliers. Where multiple acceptable points existed between all three measures, selection was based on visual comparison of projections. I assessed these projections for signs of overfitting to presence localities and for the degree to which projections realistically depicted lynx distribution in Washington State as compared to placement of lynx critical habitat and LMZs. Where there was no such evidence of overfitting, I selected the model that used the lower multiplier value to discourage underfitting.

Model Type Selection and Evaluation of Predictors

Following model tuning, I ran additional models to facilitate comparison of predictor importance and model types used for core habitat. To obtain models incorporating the maximum variability between subsamples, I re-ran each of the model types for all 200 subsamples, suspending cross-validation procedures. Predictor jackknifes, which are indicative of standalone predictor importance, were produced only for the proximal model types and were averaged across all 200 modeled subsamples for each model type. I also averaged the training AUCs, omission rates, and model projections.

I then compared core-habitat model types following tuning using model-fit metrics (i.e. test AUC and omission rate) averaged across the 10 iterations of cross-validation used in model tuning. I also compared them using training AUC and visual assessment of suitability projections averaged across the 200 modeled subsamples. With respect to AUC, I compared only models with the same background extent. I visually assessed all averaged projections for unrealistic representation of present-day lynx distributions. I first compared model types that dropped constraining predictors (i.e. types 1, 2, 4, and 5) to those that did not (i.e. types 3 and 6) using the averaged jackknife for model type 6 to evaluate the relative importance of constraining predictors. Next, I compared full model types 1-3 to proximal model types 4-6.

The best model was considered that which, in order of importance, (1) realistically depicted present-day lynx distribution, (2) allowed for a transboundary habitat suitability projection without sacrificing discriminatory power as quantified by training and test AUC, and (3) generalized fairly well to test data as quantified by test omission rate.

I used this final model type (i.e. the same predictors) to model travel-habitat as well, with the exception that a different background extent was used (**Figure 2.5c**), and produced an averaged predictor jackknife (n = 10) for the travel model. I compared core- and travel-habitat model performance, assessed fit of the final core- and travel-habitat models using averaged AUC and omission rates, compared averaged projections to what is thought to be present-day lynx distribution, and used the averaged jackknife for the final models to identify and rank important predictors.

Results

Model Tuning

Test AUC trends were similar between all model types, with differences in magnitude. Test AUC did not level off as the regularization multiplier was increased, instead showing more or less linear decreases with increasing multiplier values (**Figure 2.6a**). Training and test AUC differences and omission rate at the 10th percentile training presence threshold displayed similar trends between model types, again with differences in magnitude (**Figure 2.6b, d**). High AUC differences and omission rates occurred at lower regularization multipliers, with an initial steep drop off followed by apparent leveling out. Due to instability in the omission rate at the minimum training presence threshold (**Figure 2.6c**), this measure was not used as a tuning threshold selection criteria.

Full models (i.e. types 1-3) demonstrated comparatively larger training and test AUC differences (**Figure 2.6b**) and omission rates (**Figure 2.6c, d**) than proximal models (i.e. types 4-6). Due to inflated AUCs, training and test AUC differences were exceptionally small. However, differences in training and test AUC were greatest for model type 1and smallest for model type 5. Omission rates at the 10th percentile training presence threshold were highest for model type 3, beginning at 55% at a regularization multiplier of 0.25 and dropping to a minimum of 17.5% at a regularization multiplier of 20. Between a multiplier of 4 and 20, these rates were lowest for model type 5, with a minimum value of 10.0%.

Measures of fit were informative and I was able to deduce where reasonable trade-offs in complexity vs. simplicity may be found. **Table 2.3** summarizes the regularization multipliers selected for each model type based on the analysis strategy described previously, also providing the regularization multiplier values that were considered. Visual assessments were helpful in determining the best regularization multiplier for each model type. Model predictions differed greatly between selected regularization multipliers. Examples of projections at selected multiplier values for four model types are provided in **Figures 2.7 - 2.10**. Full models (i.e. types 1-3) appeared overfit to the observations below the highest regularization multiplier thresholds identified in **Table 2.3** (**Figures 2.7** and **2.8**). Proximal models (i.e. types 4-6) appeared overfit below the lowest regularization multiplier thresholds identified in **Table 2.3** (**Figures 2.9** and **2.10**), with one exception noted in **Table 2.3**.

Although in some cases measures of fit improved marginally at higher regularization multiplier values, projections also diminished in discriminatory ability at these higher values, based both on AUC (**Figure 2.6a**) and on visual assessment (**Figures 2.7 - 2.10**).

Table 2.3. Results of model tuning showing the regularization multiplier values selected for each model type

Model Type Number	Coincident Level Off Point(s) for All Three Measures	Selected Regularization Multiplier Value
1	6, 15	15
2	15	15
3	4, 10	10
4	2	*4
5	4, 15	4
6	6	6

* For model type 4, projections done with a regularization multiplier (RM) value less than 4.00 appeared overfit to the areas of training data (**Figure 2.9**). Consequently, although most overfitting measures appear to level out near a RM of 2.00, 4.00 was selected instead as the next highest multiplier.

The travel-habitat model was tuned using only proximal model type 4 (i.e. constraining predictors dropped). Test omission rate at the minimum training presence threshold appeared more stable between multipliers (**Figure 2.11c**), as did other measures (**Figure 2.11**). Thresholds in measures of fit suggested that the default regularization multiplier value of 1 was appropriate for the travel-habitat model.

Model Selection

Effect and Importance of Constraining Predictors

All tuned, cross-validated, core-habitat models had similar predictive ability and generalizability (**Tables 2.4** and **2.5**, **Figure 2.14**). Although test AUC was higher for models that did not drop constraining predictors (i.e. types 3 and 6), the differences were small (**Table 2.4**). Omission rates at lower cumulative thresholds were closer to expected omission rates for models that did not drop constraining variables (i.e. types 3 and 6) (**Figure 2.14**), suggesting that these models generalized better to the test data at the extremes of the suitability gradient. Model types that dropped constraining predictors (i.e. types 2 and 5) showed very little perceptible improvement over model types that did not (i.e. types 3 and 6) across higher cumulative thresholds (**Figure 2.14**). However, differences in generalizability are so slight that a clear ranking cannot be established.

In examining training AUC for the expanded sample set (n= 200) models, the same patterns are evident, with the models that included constraining predictors having slightly higher training AUC, indicating small increases in discriminatory power (**Table 2.5**). The highest AUC difference occurred between full model types that dropped (i.e. type 2) and did not drop (i.e. type

3) constraining predictors (**Tables 2.4** and **2.5**), suggesting that the full models relied more heavily on the constraining predictors than the proximal models.

Table 2.4. Mean test AUC and omission rate (n = 10) for all tuned, cross-validated models with the constrained background extent

	Test AUC (SE)		**Omission Rate (10th percentile) (SE)**	
	Proximal	**Full**	**Proximal**	**Full**
No Drop	0.9832 (0.0021)	0.9834 (0.0028)	0.155 (0.051)	0.195 (0.058)
Drop	0.9830 (0.0022)	0.9753 (0.0029)	0.100 (0.056)	0.120 (0.051)

* *No drop* refers to models that dropped geographically constraining predictors, whereas *drop* refers to models that did not. *Full* refers to the full predictor set including the expanded set of climatic variables and *proximal* refers to the proximal predictor set of preselected predictors. SE = standard error.

Table 2.5. Mean training AUC (n = 200) for all tuned models with the constrained background extent

	Training AUC (SE)	
	Proximal	**Full**
No Drop	0.9855 (0.00013)	0.9870 (0.00014)
Drop	0.9852 (0.00012)	0.9808 (0.00022)

* *No drop* refers to models that dropped geographically constraining predictors, whereas *drop* refers to models that did not. *Full* refers to the full predictor set including the expanded set of climatic variables and *proximal* refers to the proximal predictor set of preselected predictors. SE = standard error.

In terms of standalone explanatory power of constraining predictors for the proximal model (i.e. type 6), 30-year maximum burn severity had the lowest power of all predictors, April 1 SWE had low to intermediate power, and vegetation type had high explanatory power (**Figure 2.12**). However, exclusion of either vegetation type or April 1 SWE from the model did not substantially reduce explanatory power of the model. For full models, visual comparison of models that dropped (i.e. type 2) vs. did not drop (i.e. type 3) constraining predictors revealed minimal dissimilarities within shared prediction extent (**Figure 2.13b, c**), with suitable habitat appearing only more diffused within the projections that used model type 3. Dissimilarities between the proximal models (i.e. types 5 and 6) (**Figure 2.13e, f**) were more pronounced, with higher prevalence of suitability predicted for the models that included constraining predictors (i.e. type 6). However, location and shape of areas with highest suitability are highly similar between both types of models. Models that included constraining predictors are not compared to models (**Figure 2.13**) that did not and that used the full background extents (i.e. types 1 and 4) owing to the limitations imposed by the differing background extents. Given the similarity between predictive ability and the predictions, the broader research potential of the transboundary model, the constraining predictors were dropped from the final model.

Full vs. Proximal Model Types

With constraining predictors eliminated, proximal models (i.e. types 4 and 5) had, on average, higher training and test AUC than full models (i.e. types 1 and 2), although differences were slight and difficult to interpret given inflation. Based on cross-validated models, test omission rates for proximal model types 4-6 were closer to predicted omission rates across cumulative thresholds than those for full model types 1-3 (**Table 2.4**, **Figure 2.14**), suggesting improved fit. Habitat projections were similar with one key difference. Namely, the proximal models generally predicted higher habitat suitability in more northward areas, including in BC, than the full models (**Figure 2.13**). Full models generally predicted relative suitability above the BC border that was much less improved from projections within LMZs than it was for proximal models. Based on this analysis, model type 4, which used the proximal predictor set, the full background extent, and dropped the constraining variables, was selected as the final core-habitat model because it best matched model selection criteria established in the methods.

Final Models

Model Fit and Extrapolation

The final core-habitat model had high training AUC (0.9798) when averaged across all 200 subsamples. For the subsample subject to 10-fold cross-validation, I also observed high average training AUC (0.9814) and test AUC (0.9778). These values would ordinarily indicate an exceptional fit, as in a logistic regression or other model with binary outcomes, but AUC values in both cases are certainly inflated as a result of large available fractional area, an artifact of the choice of background. However, omission rates were close to expected rates (**Figure 2.14d**). They were highly variable as evidenced in the standard deviation of the test omission rate (**Figure 2.14d**), but less variable than some of the other model types. Environmental novelty (i.e. the degree to which values throughout the study area are dissimilar to those in the training area) depicted in MESS outputs for the core-habitat projection is fairly low throughout with strong similarity through parts of the North Cascades, the Okanogan Highlands, the Blue Mountains, and the Cascades to the south (**Figure 2.15a**). A small degree of novelty is noted where higher suitability is predicted in BC and in the Willowa Mountains.

AUC values for the travel model did not appear to suffer from inflation. Average test AUC (0.6412) was smaller than training AUC (0.7583), suggesting that models did not generalize as well to the test bins of cross-validation. However, values in this range indicate a model with higher than random discriminatory power (**Figure 2.11a**). Environmental novelty (i.e. the degree to which values throughout the study area are dissimilar to those in the training area) associated with the travel-habitat projection is higher than that for the core-habitat projection, with highest uncertainty within the Puget Lowlands, the Columbia Basin, and the northeastern corner of the study area (**Figure 2.15b**).

Predictor Importance

Based on the average predictor jackknife for the core-habitat model (**Figure 2.16a**), frost-free period (54.2%), degree-days above 5°C (52.1%), and degree-days below 0°C (51.9%) had the highest standalone predictor importance, followed by the mean warmest month temperature (43.3%), Hargreaves Climatic Moisture Deficit (26.2%), distance to primary roads (19.5%), summer precipitation (16.0%), and distance to secondary roads (12.4%), in that order. Slope, aspect, compound topographic index, and distance to local roads had less than 2% standalone explanatory power each. The model lost the greatest amount of explanatory power when distance to primary roads (8.1%) or degree-days below 0°C (4.9%) were removed from the model, suggesting that these predictors are particularly important in projecting suitability. Confidence intervals on jackknife values were small, suggesting that predictor importance varied minimally between modeled samples (i.e. predictors are stable).

Important predictors were similar within the travel model (**Figure 2.16b**), with some important distinctions. Standalone predictor contributions are lower, whereas explanatory power losses on removal of certain predictors are higher. Frost-free period (23.5%) and degree-days above 5°C

(24.0%) once again have the highest standalone explanatory power. However, mean warmest month temperature (22.2%) ranked higher, followed by degree-days below 0°C (12.1%), distance to primary roads (10.1%), and Hargreaves Climatic Moisture Deficit (8.2%). Distance to secondary roads (3.2%) and summer precipitation (0.4%) are diminished in importance. Slope, aspect, compound topographic index, and distance to local roads see small relative increases, but remain low with less than 5% standalone explanatory power. As with the core-habitat model, eliminating distance to primary roads reduces explanatory power the most (24.1%). However, other predictors appeared to be important based on loss of explanatory power upon removal, including distance to secondary roads (17.6%), slope (8.0%), compound topographic index (7.7%), and summer precipitation (7.6%), followed by the remaining predictors at less than 7% each. Although mean warmest month temperature ranked high in standalone importance, there was little explanatory power lost without it (1.6%). Confidence intervals on jackknife values were small but larger than those for the core model, suggesting increased variability between modeled samples, although predictors are more or less stable.

Habitat Projections

Core Habitat

Core-habitat suitability projections indicate that patches of suitability are distributed throughout the study area, and in general, decrease in both size and quality along a latitudinal gradient from north to south (**Figure 2.17**). However, scattered yet small pockets of moderate to marginal suitability are predicted even at the most southern extent of the study area. Within Washington State, highest suitability is predicted mainly within the North Cascades. Moderate suitability is predicted throughout the Okanogan National Forest, extending west into Mount Baker National Forest, east into the Loomis State Forest, and decreasing to marginal suitability moving south across the Sawtooth Ridge. Somewhat surprisingly, poor to no suitability is predicted for the southwestern portion of the Okanogan-Wenatchee LMZ. However, model predictions align well with lynx critical habitat in the North Cascades (Unit 4). The model also predicts marginal suitability in northeastern portions of the Wenatchee National Forest in the Entiat and Chelan Mountains and moderate suitability within southeastern regions of the Wenatchee National Forest, particularly within the Wenatchee Mountains.

Relative suitability increases up through the North Cascades from Washington State into the Okanogan Range and the Thompson-Okanagan Plateau and then northwest into the Interior Transition Ranges of BC. The model predicts moderate to high suitability throughout the Okanagan Highlands of BC, with suitability persisting though decreasing eastward from the Beaverdell Range to the Midway Range. Suitable habitat extends through the Okanagan Highlands south into the western border of the Okanogan Highlands of Washington State, becoming marginal to poor. Although suitable habitat is believed to exist throughout portions of the Okanogan Highlands, suitability is predicted to be poor to none throughout much of this area, including areas within the Vulcan-Tunk, Kettle Range, the Wedge, Little Pend Oreille, and Salmo Priest LMZs (Stinson 2001).

Travel Habitat

The travel model predicted far greater prevalence of travel-habitat suitability than core-habitat suitability, with notable exceptions occurring along several physiographic regions, including the Puget Lowland, the Willapa Hills, the Columbia Basin, and most of the Olympic Mountains (**Figure 2.18**). Although high suitability is predicted along the Cascade Range, the suitability band narrows noticeably in the transition between the North Cascades and the south Cascades in Washington State, and again at several points along the southern stretch into Oregon. Much of the BC portion of the study area is predicted to have some degree of suitability, with noticeably high values around Birkenhead Lake, Duffey Lake, and Joffre Lakes Provincial Parks. Other areas of noticeably high predicted travel suitability include the west Okanogan Highlands, much of the Blue Mountains of Oregon, and the portion of the Purcell Mountains included in the study area.

Although travel habitat may not be synonymous with actual landscape resistance to lynx movement, there are likely to be similarities. Travel-habitat projections suggest that functional connectivity within the Okanogan LMZ is likely to be high presently, with the greatest possible exception being within the southwestern portion of the LMZ where habitat suitability is generally projected to be low (**Figure 2.18**). The Twisp River valley may represent a small barrier between moderately suitable habitats to the north and marginally suitable habitats to the south. The Methow River may function similarly. Lake Chelan likely represents a substantial barrier that lynx may navigate around to the east if dispersing into the south, where habitat suitability is also fairly low. Projections suggest that low elevation valleys may be avoided during travel, including those running roughly north to south between habitats in the northeastern portion of the LMZ and those in northwestern potion of the LMZ. These areas may include valleys surrounding tributaries of the Chewuch River, such as Andrews Creek and Lake Creek, and valleys further to the west following Lost River. It is possible given the distribution of suitable habitat that lynx movements emanating from habitats in the general region of the Pasaytan Wilderness may be offset to the north where valleys bottoms are narrower and less deep.

Discussion

Habitat models produced augment existing work by identifying areas where potential suitability is high, identifying differences between local-scale and regional-scale habitat-selection drivers, providing a transboundary model of habitat suitability for this region, and quantifying regional-scale selection drivers in a manner that allows models to be projected into future climates. Here, for both the core- and travel-habitat models, I discuss the imports and caveats of model tuning, model selection, predictor importance, and model realism, framing each within a broader context and comparing results to previous studies where applicable. I end by discussing the caveats, assumptions, and recommendations for future research. Management and conservation applications should make use of the limitations discussed here to contextualize resulting suitability projections.

Model Tuning

Model tuning proved to be essential to establishing a balance between fit and complexity, as appropriate levels of regularization for all core-habitat model types exceeded default regularization levels set in MAXENT. This represents a significant improvement over typically employed methods in model applications using MAXENT, in which finding adequate levels of regularization is frequently not addressed (Elith et al. 2011, Radosavljevic and Anderson 2014). Differences in measures of fit were consistent with those expected to result from the variations in complexity of each modeling approach. The size of the background extent and the number of features clearly increased model complexity (**Figure 2.6**). For full models (i.e. using the full predictor set), measures of fit and visual assessment (**Figures 2.7** and **2.8**), not surprisingly, suggested a need for more regularization than with proximal models (i.e. those using the proximal predictor subset).

For core-habitat models, behavior of threshold-independent and threshold-dependent measures was similar to those of Radosavljevic and Anderson (2014) with the exception that test AUC did not level off as the regularization multiplier was increased, instead showing more or less linear decreases with increasing multiplier values (**Figure 2.6a**). However, high AUC differences and omission rates occurred at lower regularization multipliers as expected, with an initial steep drop off followed by apparent leveling out. Although these patterns were similar to those of Radosavljevic and Anderson (2014), trends were also punctuated by fluctuations indicative of some instability in the measures (**Figure 2.6b, c, d**), especially test omission rate at the minimum training threshold (**Figure 2.6c**). Clear thresholds in model-fit metrics were less readily identified due to this instability. These minor instabilities in model tuning metrics may have been a result of some residual spatial autocorrelation within the observation data even following spatial rarefication.

Geographically Constraining Predictors

Although April 1 SWE and potential vegetation type were of moderate importance in the models including them, differences in model performance between models that used these predictors and those that did not were slight. Models that did not drop constraining predictors had somewhat higher discriminatory power (i.e. AUC) and somewhat lower generalizability (i.e. omission rate fit) across higher cumulative thresholds, with higher generalizability at the low end of suitability thresholds. Differences in generalizability were perhaps due to high importance of the constraining predictor vegetation type, a categorical variable. As abstractions of continuous phenomena, categorical variables can introduce problems into habitat suitability models because relationships between classifications are not considered (Parisien and Moritz 2009). Such data can fragment the environmental space and limit transferability of that space outside of the classes

(Parisien and Moritz 2009). Thus, vegetation type may have consumed explanatory power and limited applicability of the trained models. Nevertheless, differences in generalizability were so slight that a clear ranking could not be established.

Small differences in AUC (**Tables 2.4** and **2.5**) and apparent similarity of projections between models that dropped and did not drop constraining predictors (**Figure 2.13**) may suggest that the other predictors are capable of implicitly capturing these drivers in the absence of more direct proxies. Specific explicit mechanisms tied to vegetation type and snow quality may have been implicitly captured in the other predictors included in the models, such as degree-days below 0°C, mean temperature of the warmest month, growing degree days (i.e. degree-days above 5°C), or mean annual summer precipitation.

Given the similarity between predictive ability and the projection maps and the broader research potential of the transboundary model, the constraining predictors were dropped from the final model. Dropping these predictors allowed projections to expand north of the BC border and extended the applications of subsequent analyses to transboundary suitability and connectivity, areas in need of exploration for lynx in Washington State. By providing a transboundary model of habitat suitability for this region, my research expands on existing work, as transboundary projections of habitat suitability at the scale of this analysis did not previously exist (McKelvey et al. 2000c, Koehler et al. 2008, Maletzke et al. 2008, Peers et al. 2014, Vanbianchi 2015).

Conceptualization of Regional-Scale Selection Drivers

Based on all three criteria established in the methods (i.e. realism of projections, training and test AUC, and generalizability), proximal models outperformed full models. The proximal model that dropped constraining predictors (i.e. type 4) best matched model selection criteria established in the methods. This model depicted present-day lynx habitat suitability more realistically than full models, allowed for transboundary projections without much loss of discriminatory power, and had improved predictive power and generalizability over the full models. For models with constraining predictors dropped, proximal models bested full models, but only slightly, in discriminatory ability (i.e. AUC) (**Tables 2.4** and **2.5**). Projections also appeared more realistic for proximal models, predicting higher habitat suitability in more northward areas, (**Figure 2.13**) and generalizability to test data was improved (**Figure 2.14**). Habitat suitability that increases along a latitudinal gradient is more consistent with previous studies of lynx distributions (see *Chapter 1*).

Given the importance of retaining mechanistic drivers when extrapolating to future climates, I retained the model with the highest observed ability to extrapolate accurately based on visual assessment. Extrapolation outside the range of predictors is always associated with uncertainty, and as Elith et al. (2011) cautioned, screening potential candidate variables to limit responses to more proximal drivers may have improved projections outside of the training area in this case. As there is no need nor justifiable reason to restrict the background extent of models that dropped the constraining predictors to the constrained extent, other than to compare model-fit metrics to models that did not, models that used the constrained background extent and dropped constraining predictors were eliminated from consideration in model selection.

Regional-Scale Selection Drivers

Results indicate that habitat selection at a regional scale is different than habitat selection at either local scales or very broad scales. At the scale and extent of this analysis, results were generally consistent with expectations that snow longevity and condition and environmental conditions that allow productive understory would be important, whereas results were not consistent with expectations that slope, aspect, compound topographic index, local roads, and 30-year maximum burn severity would be important.

Limitations existed with respect to interpretation of important predictors in the model. As relationships may change over the shape of the response curves, it is tenuous to interpret magnitude and coefficient sign of features included in the model without evaluating these response curves. It is equally tenuous to compare any interpretations on positive or negative selection to previous studies, as the ranges of values in predictors can vary along with the units of measure. As the end goal of this study is to project habitat suitability into the future rather than provide another evaluation of lynx habitat selection, response curves were not evaluated. As a result, this study is confined to evaluating the relative importance of predictors, comparing this to existing studies, and discussing likely mechanisms.

Frost-free period and degree-days above 5°C were important predictors in the final core-habitat model as was degree-days below 0°C. These variables are indirectly tied to both snow amount and quality and productivity of understory during the growing season, but their importance suggests that at the very least lynx select not only for temperature but also for freeze-thaw dynamics (i.e. degree-days below 0°C). This is consistent with previous studies showing snow longevity and firmness to be important (Murray and Boutin 1991, von Kienast 2003, Stenseth et al. 2004, Hoving et al. 2005, Gonzalez et al. 2007, Squires et al. 2010, Peers et al. 2013), and with theories on the advantages of lynx morphology and hunting effectiveness (Murray and Boutin 1991, Buskirk et al. 2000b, Interagency Lynx Biology Team 2013) and snowshoe hare (*Lepus americanus*) morphology and pelage (Koehler 1990b, Buskirk et al. 2000b, Wirsing and Murray 2002, Interagency Lynx Biology Team 2013, Mills et al. 2013) in areas with increased snow.

Findings on the importance of degree-days below 0°C may also lend support to the hypothesis that, where lynx overlap with competitors, crusted snow reduces the competitive advantage that lynx have because of their long legs and low foot loadings (Buskirk et al. 2000a), but this is not certain as effect direction has not been established. Several studies have assessed relationships with snow firmness, finding that lynx select for firmer snow than bobcats or coyotes (*Canis latrans*) where ranges overlap, but that lynx will use harder, shallower snow when not in competition (Murray and Boutin 1991, von Kienast 2003, Peers et al. 2013). This may be due to niche displacement between bobcats, coyotes, and lynx, with bobcats and coyotes preferring shorter lived, more easily traversed snow conditions (Murray and Boutin 1991, Peers et al. 2013).

All variables included as surrogates for productivity of understory vegetation, except for compound topographic index, were important in the final models, suggesting that productivity of understory vegetation may play a role in regional-scale habitat selection. Mean annual summer precipitation was of marginal importance whereas mean temperature of the warmest month was of moderate importance in the model. This is consistent with previous research. Vanbianchi (2015) found growing season precipitation to be the most influential predictor in the model, and heat load index, a measure of temperature based on slope and aspect, to be of marginal importance. In jackknife estimates, the broader-in-extent Peers et al. (2013) study found maximum temperature of the warmest month to be the most influential variable when considered alone. Similar to the marginal importance of summer precipitation in my models, Peers et al. (2013) found that precipitation of the warmest quarter had marginal importance.

Hargreaves Climatic Moisture Deficit was also of moderate importance in the models. This variable is the sum of the monthly difference between reference evaporation calculated using the

Hargreaves temperature-based approach and precipitation (Wang et al. 2012). It measures the additional moisture needed for vegetation growth to avoid drought impacts (Wang et al. 2012). Although Vanbianchi (2015)'s finding on the importance of moisture was based on an aspect- and slope-based surrogate for moisture dynamics, compound topographic index (< 2% explanatory power in my core-habitat model), this predictor is more heterogeneous locally than Hargreaves Climatic Moisture Deficit, a broader-scale indicator of moisture dynamics. Given the larger extent of my models, importance of this variable is consistent with previous results on the importance of moisture dynamics and suggests that precipitation is not the only factor to consider in these moisture dynamics. No other studies to my knowledge have used Hargreaves Climatic Moisture Deficit as a predictor of lynx habitat suitability.

Contrary to expectations, slope was not relevant at a 1-km grid-cell size for core habitat, with less than 2% standalone explanatory power. Although lynx may have selected for slope within home ranges, by itself, slope was not a good predictor of the placement of use clusters. Presence-only model results are contingent upon grain size and extent from which available habitat is selected. Most studies on lynx in Washington that found slope to be relevant were smaller extent habitat-selection studies done at a smaller grain size (McKelvey et al. 2000c, von Kienast 2003, Koehler et al. 2008, Maletzke et al. 2008). One exception to grain size is Vanbianchi (2015)'s core-habitat selection model, wherein slope was the second most important predictor, even at a grid-cell size of 810 km. Nevertheless, the extent from which available habitat was selected was still much smaller. I attribute the difference in results primarily to the size of the available habitat (i.e. the background extent used in my study) as compared to the area of the training data, especially given the degree of local heterogeneity present in the slope variable. As the aim of this study is to identify habitat suitability at a regional-scale across a large study area, as opposed to identifying the causes of habitat selection within the vicinity of training observations, minimal reliance on slope is an acceptable and informative result.

Some studies have identified aspect (McKelvey et al. 2000c) and compound topographic index (Vanbianchi 2015) as important predictors. My study found them to be negligible influences, likely for the same reasons that slope ranked low in my model (i.e. fine-scale heterogeneity combined with an approach that evaluated regional-scale selection). However, McKelvey et al. (2000c) found that lynx select for aspect mainly during summer. As such, that my model was a combined and not seasonal model could have also reduced the importance of aspect.

It is noteworthy that in proximal models including burn severity, this predictor had the lowest possible explanatory power of all predictors. Given that the predictor is a 30-year maximum, this cannot be taken to imply that burns are irrelevant to habitat selection at this scale and extent. Though difficult to pinpoint, there are a multitude of possibilities as to why lynx did not select for burn severity. For example, the predictor judges maximum severity based on multiple fires occurring across the 30-year time period, but does not contain information on timing of fires or on recovery rates. Lynx in Washington State have been shown to avoid burns less than 15 years old (Koehler et al. 2008, Maletzke et al. 2008, Vanbianchi 2015) but not older burns regardless of severity (Koehler et al. 2008, Maletzke et al. 2008, Vanbianchi 2015). Following a sufficient period of time after a fire, understory in burned areas, especially within vegetation types adapted to frequent fire such as lodgepole pine, can reestablish, increasing the foraging potential for lynx for a time period (Interagency Lynx Biology Team 2013). Consequently, the 30-year resolution of the predictor may have failed to capture responses that occur over a smaller time frame.

Another explanation may be that the degree of overlap of lynx telemetry points with high severity burns on the edge of the 2006 Tripod Fire, the largest fire within the 30-year period, led the model to conclude no preference. More realistically, recovery rates can differ throughout a burned patch. For example, recovery may proceed more quickly along the perimeter of a fire where seed sources are readily available. Variability in recovery rate is not captured in the maximum burn severity predictor. Consistent with this explanation, Vanbianchi (2015) found that within new burns, lynx selected for burn perimeter, fire skips, and residual live trees, but avoided severely burned areas. Given that lynx use of burns is multi-faceted and complex and models of fire are necessarily stochastic, inclusion of wildfire in this rich a detail is unlikely to bring much to models constructed primarily to project habitat suitability into future climate spaces.

Distance to primary roads (i.e. freeways) and distance to secondary roads (i.e. highways) were important predictors in the model, suggesting that lynx may factor in proximity to freeways and highways when establishing home ranges. However, this result is questionable considering that highways and, to a greater extent, freeways, are fairly distant from the core of home ranges where presences were observed. Importance may be more likely attributable to mountainous areas being unsuitable for freeway construction than to selection or avoidance by lynx and given the sparsity and somewhat predictable pattern of freeways and highways within and near the available background extent, coincidence cannot be ruled out. Lynx have been known to cross highways with some regularity, although a few studies have found that they do so at rates less than those of random expectation (Apps et al. 2007). My study found local roads to be unimportant (< 2% explanatory power). Evidence of road use or preference in previous studies is mixed. Some studies have found avoidance (Fuller et al. 2007), whereas other studies have found neutrality of lynx with respect to roads (McKelvey et al. 2000b, Squires et al. 2008). Even if lynx neither prefer nor avoid roads, this does not mean mortality on them is not an issue (Interagency Lynx Biology Team 2013).

Comparing Travel-Habitat Selection

Although differences in relative importance of predictors was noted between the core- and travel-habitat models, both predicted high relative importance of frost-free period, degree-days above 5°C, degree-days below 0°C, and distance to primary and secondary roads. However, predictors in the travel model had lower explanatory power (i.e. weaker dependence) overall, discriminatory ability was marginal, prevalence of suitability was higher, and confidence intervals around predictor importance were larger. This disparity may reflect the more versatile nature of lynx travel-habitat selection compared to core-habitat selection. This interpretation is consistent with previous research indicating increased dispersal plasticity for Canada lynx (Vanbianchi 2015), which has been observed for the Iberian lynx as well (Gastón et al. 2016). Lynx are known for their long-distance dispersal abilities of up to 1100 km (Slough and Mowat 1996) and have been observed to cross frozen lakes, desert, farmland, highways, and major rivers during dispersal (Ward and Krebs 1985, Aubry et al. 2000). Additional possibilities for low discriminatory power include poor discrimination owing to seasonal differences in travel-habitat use, which were not separated for travel-habitat modeling, or failure to include predictors that act as the primary drivers of travel-habitat selection.

Realism of the Final Core-Habitat Model

The final core-habitat model had very high discriminatory power (AUC = 0.98), good generalizability, realism in visual assessments (with the possible exception of the Okanogan Highlands), and low environmental novelty throughout the study area. For the most part, areas currently thought to provide prime lynx habitat are predicted to be suitable. However, my results suggest that either past habitat selection in northeastern Washington was fundamentally different or that these areas are no longer suitable.

Although recent evidence is lacking, lynx populations have historically occurred in the Kettle Range (Stinson 2001). The notable absence of suitability within the Okanogan Highlands is concerning. A history of over-trapping is thought to be the reason that evidence of presence is scarce, not poor suitability (Stinson 2001, Koehler et al. 2008). One of the limitations of this study is the localized nature of the presence data, especially given the need to extrapolate relationships to other areas. If habitat selection outside the training areas is significantly different, these projections may not accurately reflect suitability in areas that are too far from the presence data, including the Kettle Range. Failure to predict suitability in this area can scarcely be attributed to environmental novelty, as MESS maps indicate fairly low environmental novelty throughout the study area. This suggests that it is possible that habitat selection in regions farther to the east was fundamentally different in some way when lynx were present or that these areas are no longer suitable. Nevertheless, I join Koehler et al. (2008) in recommending that a feasibility assessment be conducted prior to attempts to reintroduce lynx to this area.

Finally, marginal-to-high, yet patchy suitability is also predicted throughout the southern end of study area where lynx populations are no longer believed to exist. However, considering that connectivity may be restricted, it is not a given that these areas would support populations.

Caveats, Assumptions, and Recommendations

Although AUC values for the core-habitat models were certainly inflated, omission rates and visual assessment of projections suggest that model discriminatory power is good. Despite this, perhaps the most limiting angle of the analysis was the lack of a sufficiently sized independent test dataset by which to validate the model, particularly with respect to areas where training data were lacking. Cross-validation procedures relying on non-independent test data were used in lieu of such a dataset. More distributed observations would have also improved the models in several ways. First, observations distributed over a broader extent would have allowed for an increase in available environmental space, placing some limitations on extrapolation and reducing the inflation in training and test AUC values that I have attributed to the broadness of the background extent relative to the observation points. Second but foremost, observations from areas within the Okanogan Highlands would have likely resulted in more robust models. Given this, I recommend evaluating for differences between habitat-selection drivers in regions farther from the Loomis State Forest and Black Pine Basin to determine whether lynx in these regions are likely to respond similarly or if novel conditions in these environments point to differences in selection drivers.

For this analysis, habitat selection was assumed to be equivalent to habitat suitability. Ecologically speaking, although this assumption is made frequently in species distribution modeling, these two concepts are not interchangeable. Although studies that assess habitat suitability based on patterns of occurrence are often used as an empirical basis for assessing quality of habitat, it is important to remember that animal avoidance or selection is not necessarily always a proxy for fitness gains or costs. Two examples of why habitat suitability may be different than habitat selection are mortality risks and competition dynamics. Although perceptions of mortality risk can influence selection behavior (Gastón et al. 2016), it cannot necessarily be assumed that lynx select for environmental conditions that reduce mortality risk. An example is lynx harvest practices in BC, a significant risk factor even where habitat suitability is otherwise high. Furthermore, models include predictors relevant to snow conditions, which are thought to mediate niche displacement between lynx and their primary competitors, bobcats (*Lynx rufus*) and coyotes (*Canis latrans*). However, assuming the definition of suitable habitat includes optimal foraging, any other competition dynamics that can change the overall value of an otherwise suitable habitat are not accounted for here.

Other reasons why models may not fully capture habitat suitability include intersexual and seasonal differences in selection. Models did not distinguish between male and female habitat selection, and as such, depending on the degree to which reproduction is dependent on habitat being suitable for one sex over the other, outcomes may change. The core-habitat model mixed observations from both males and females, which essentially represents an assumption of no difference. Furthermore, the core-habitat model was based on only three females as compared to eleven males, whereas the travel-habitat model was based only on observations from male exploratory movements. Selection patterns have been shown to be different between the sexes (Interagency Lynx Biology Team 2013), and as such, it is advisable to check for such differences in future modeling efforts and to consider possible differences when applying suitability projections to lynx management.

Several angles of this analysis require projections to be interpreted not as actual but as potential habitat suitability. For example, predictors incorporated to capture cover dynamics have been shown to be less related to actual cover and more related to understory biomass indices (Suchar and Crookston 2010). Furthermore, models that incorporated vegetation type, though not selected for further analysis, are based on potential vegetation most adapted to climate drivers (Sheehan et al. 2015). The authors caution that delays in transitions due to longevity of vegetation or resistance to change exist. Direct measures of habitat-selection drivers are preferable when available. However, given that ground surveys were outside the scope of the project and that there was a need to match present-day and future predictors as closely as possible, potential habitat suitability projections represent the best available tools for answering the research questions posed. As such, maps should be interpreted with some caution, especially at local scales and fine resolutions.

Limitations of this study require it to be interpreted as potential relative suitability localized to the study region (e.g. not as actual suitability or as representative of the species fundamental niche). An important distinction exists between modeling a species fundamental niche as opposed to realized niche. For a variety of reasons (i.e. lack of functional connectivity, competition dynamics, or human influence), the fundamental niche and realized niche may not coincide (Phillips et al. 2006). Use of presence data allows for the contribution of factors outside of those influencing habitat suitability. Furthermore, in models based on training data originating from a fraction of the full species range, all suitability probabilities are relative to each other, and not necessarily relative to the best habitats within the species' entire range. Thus, the outcomes produced in this study are not representative of the fundamental niche but rather of localized relative probability (i.e. the realized distribution at the southern range periphery) for this region (Pulliam 2000, Phillips et al. 2006).

Implementing masks over potentially suitable unsampled habitat likely imposed some geographic directional bias within the background sample, most prominently within the northern section of the background extent (**Figure 2.5a, b**). Although a south-shifted background sample is likely to produce a positive northern bias in habitat suitability, given the small size of the background extent relative to the sampled area compared to broader-scale habitat distribution models, this effect is likely to be minimal (Elith et al. 2011).

Further work is recommended to investigate these dynamics further, including the construction of independent models for season and sex of the individuals, use of independent test data within the study area to validate regional patterns, and examination of variable response curves to allow comparison of effect and magnitude of included predictors to previous studies.

Figures

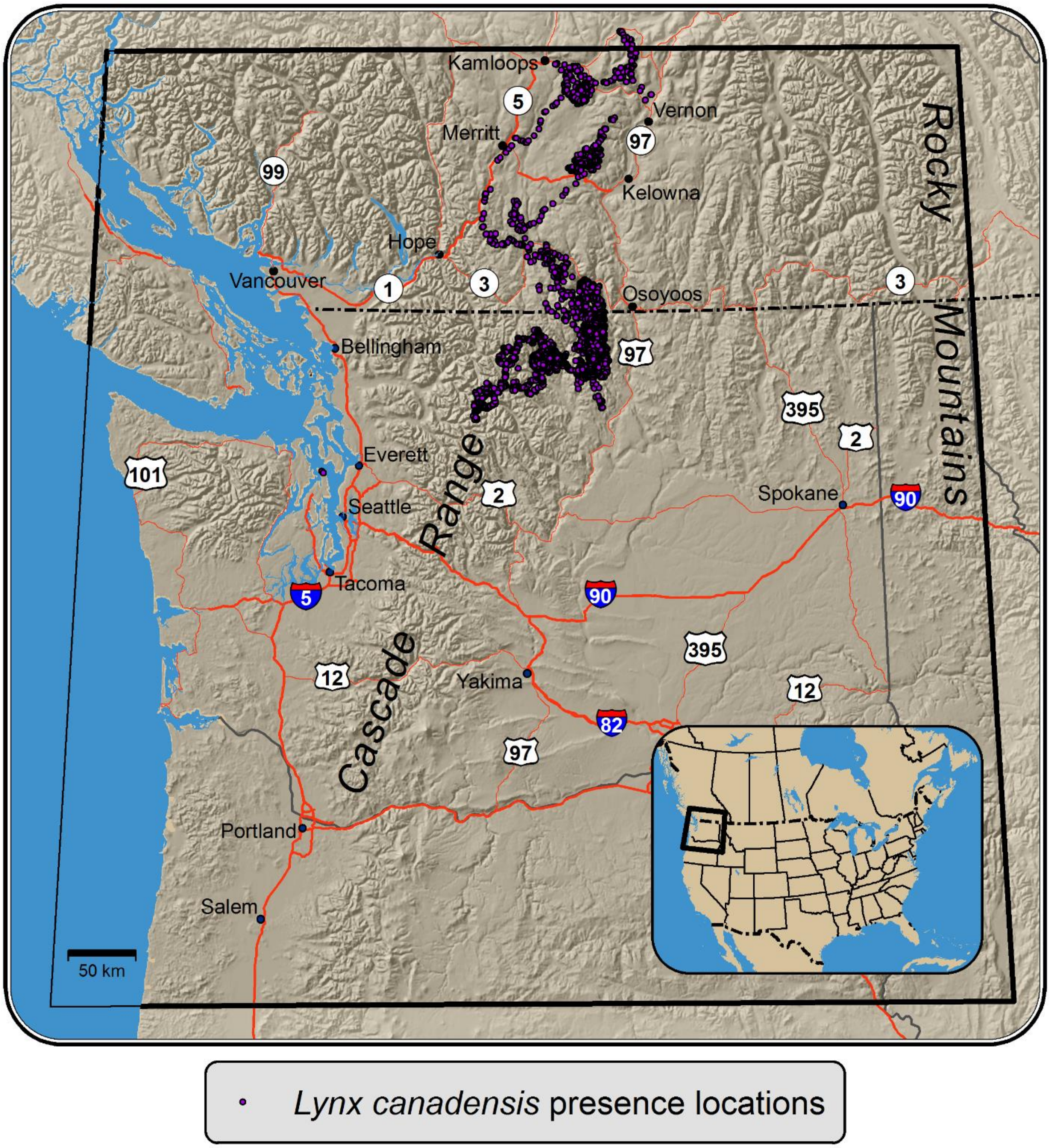


Figure 2.1. Study area showing *Lynx canadensis* Global Positioning System telemetry data.

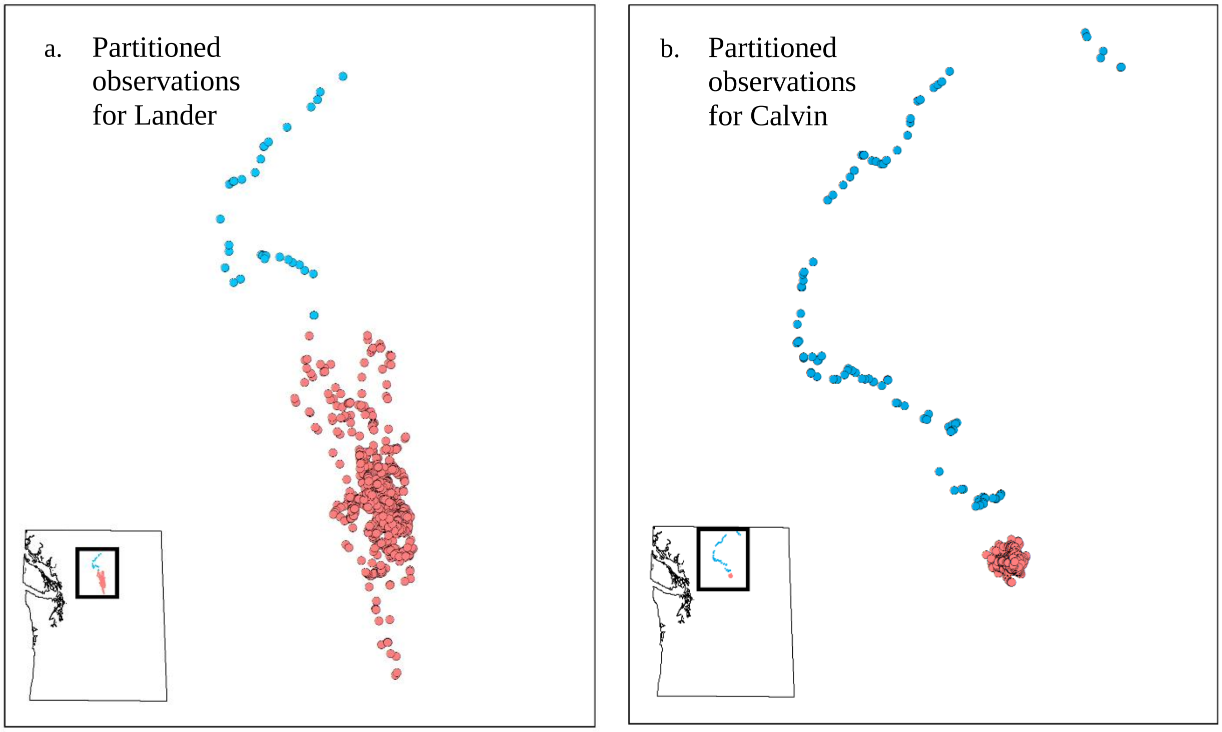


Figure 2.2. Example of partitioned *Lynx canadensis* Global Positioning System telemetry data showing exploratory movements and localized within-range movements for (a) Lander and (b) Calvin. Exploratory movements are shown as orange dots and within range movements are shown as pink dots. Observations for Calvin and Lander, two of the four male lynx that made exploratory movements greater than 35 km out of home ranges, are shown as an example of how observations were selected for both core- and travel-habitat models.

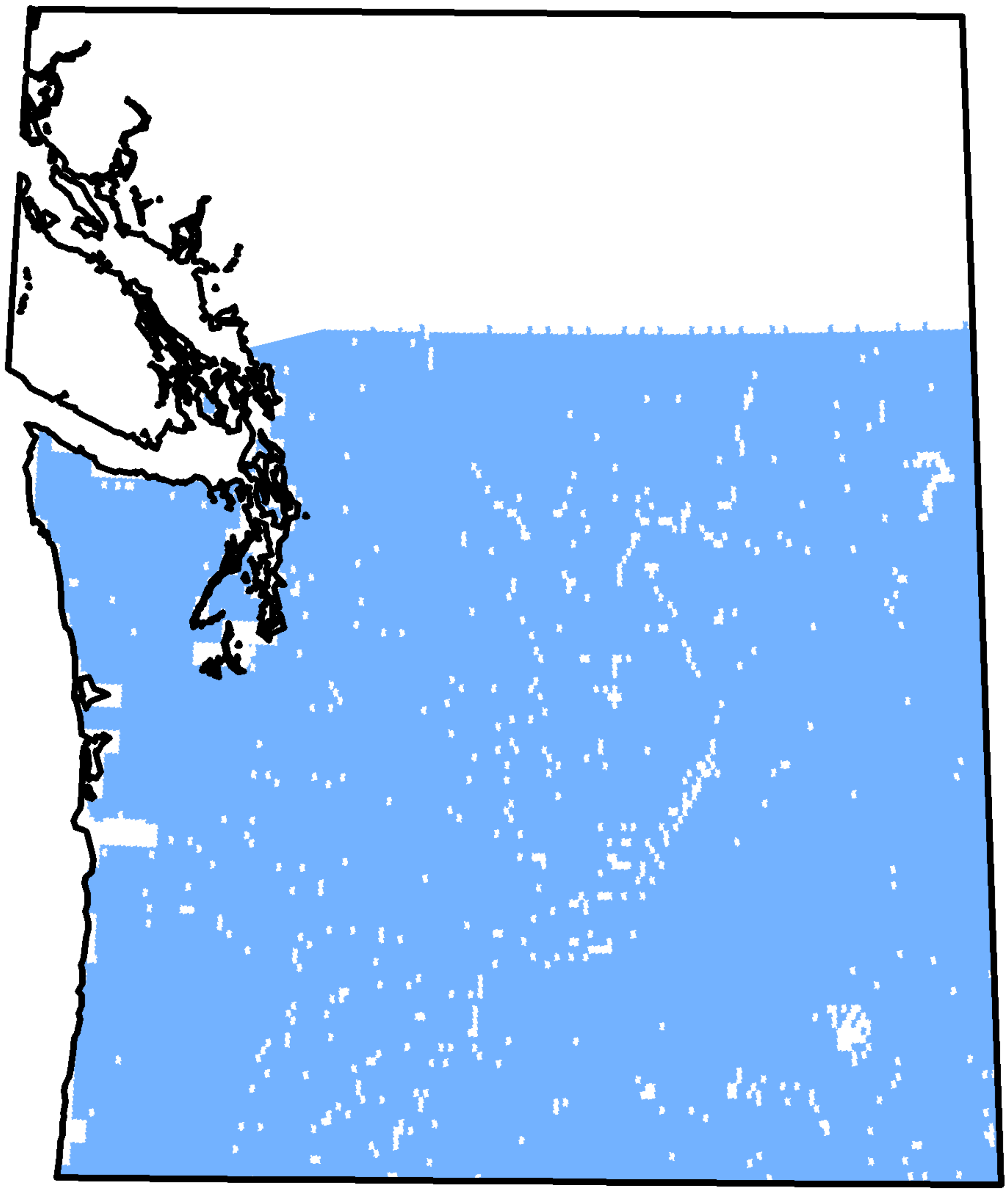


Figure 2.3. Map of the intersection of the geographically constraining predictors explored during model selection. Grid cells with data are indicated in blue; grid cells with no data are indicated in white. Constraining predictors are modal MC2 dynamic global vegetation model (DGVM) potential vegetation type, 30-year maximum burn severity, and April 1 snow water equivalent (SWE). For models that included these predictors, projections were constrained to south of the British Columbia border and grid cells where data were not available (white) could not be projected.

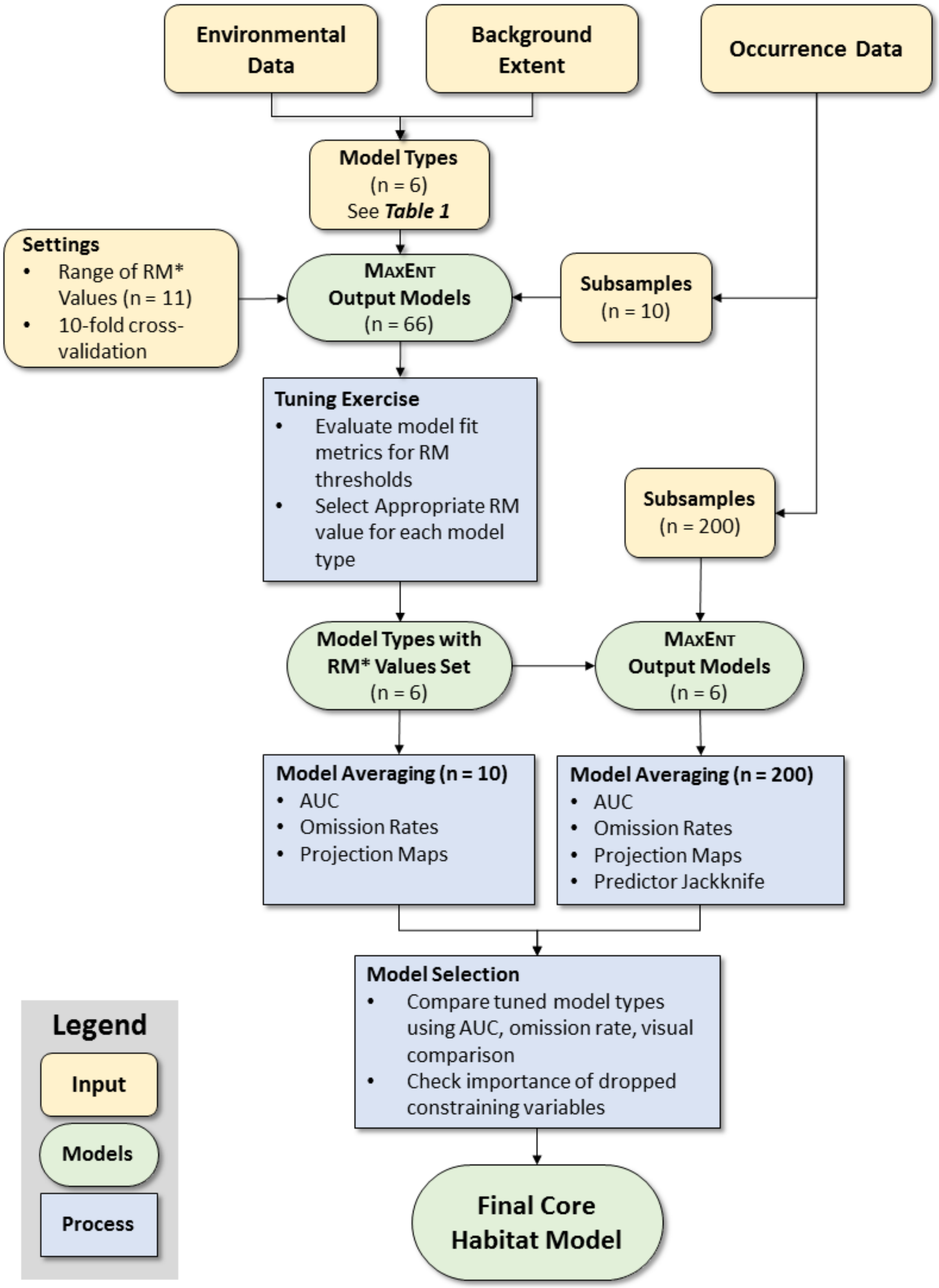


Figure 2.4. Diagram of the MaxEnt modeling, model tuning, and model selection process, beginning with selection of inputs and ending with the final core-habitat model. See *Modeling Methods* for further information. *RM = Regularization Multiplier.

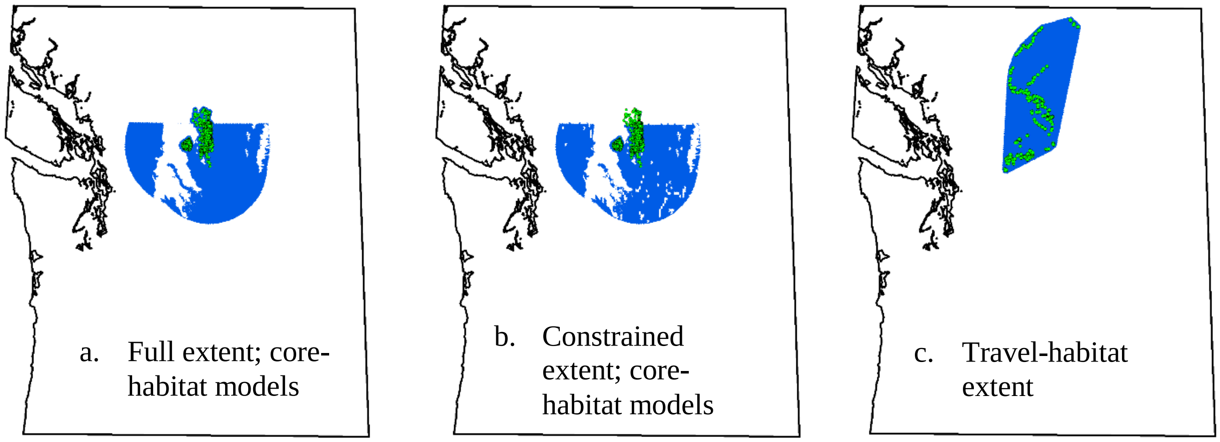


Figure 2.5. Background extents from which available locations were selected for each model type. The study area is denoted as a black polygon; background extents are in blue. The full background extent (a) was used for two core-habitat models that dropped constraining predictors, whereas constrained background extent (b) was used for four core-habitat models (two that dropped predictors and two that did not) to maintain consistency in background extent. Using the constrained background extent for some models allowed for comparison of model-fit statistics. The constrained background extent is the intersection of the full background extent with the grid cells available between the three constraining predictors (30-year maximum burn severity, April 1 snow water equivalent, and vegetation type). The entire set of resident lynx observation points used with the background extent is also shown (green). The travel-habitat background extent (c) was used only for the travel-habitat models; observations of lynx exploratory movements are shown (green).

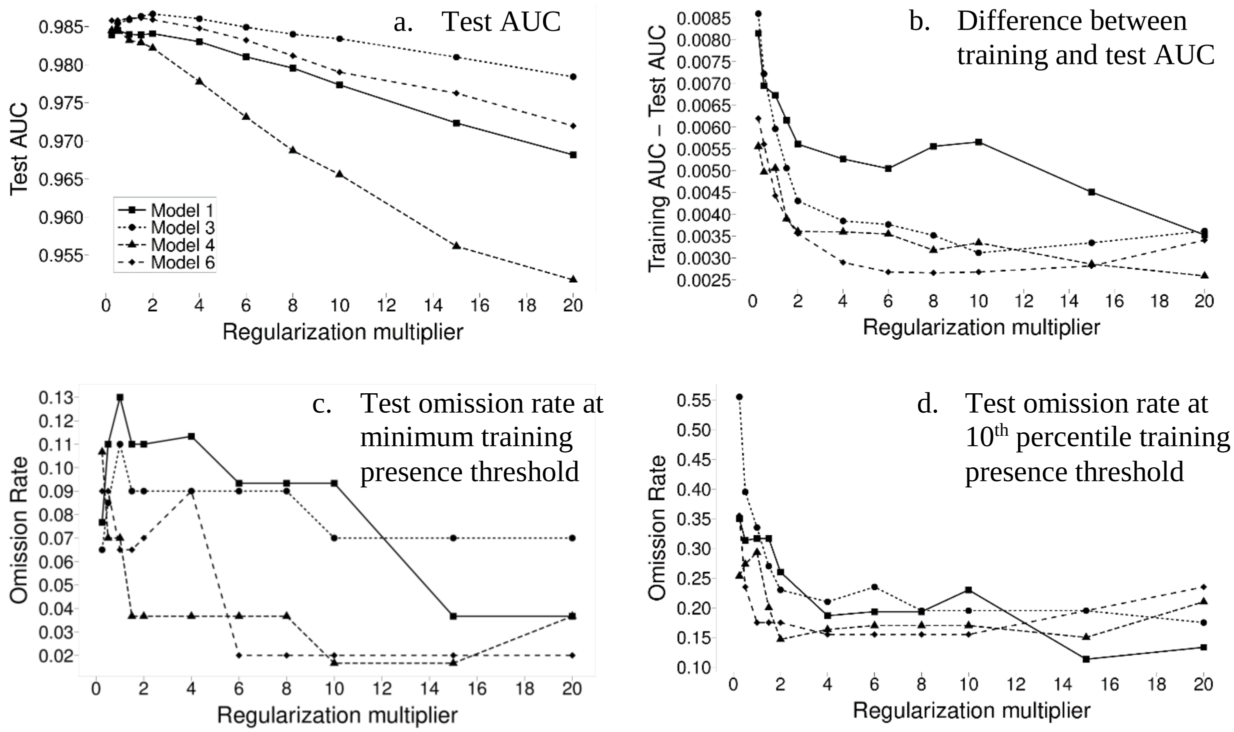


Figure 2.6. The results of the regularization multiplier tuning exercise for several approaches to *Lynx canadensis* core-habitat modeling, showing threshold-independent and threshold-dependent measures: (a) test area under the curve (AUC) (b) difference between training and AUC, (c) test omission rate at the minimum training presence threshold, and (d) test omission rate at the 10th percentile training presence threshold. See **Table 2.2** for a summary of the modeling approaches associated with each model type. For each model type, values are averaged across the 10 iterations of cross-validation of each model with a different regularization multiplier (RM) value. Test AUC refers to the discriminatory ability of each model type at each RM value. The other three measures characterize overfitting with lower values indicating improved generalizability, and possibly, underfitting. Deviations from expected omission rate (i.e. zero at the lowest presence threshold and 10% at the 10th percentile presence threshold) were used to quantify overfitting, as were differences between training and test AUC. For models that dropped constraining predictors, plots only show results from models that used the full background extent (i.e. types 1 and 4). However, models that dropped constraining predictors were run with the constrained background extent as well (i.e. types 2 and 5) and behaved similarly with respect to selected RM values.

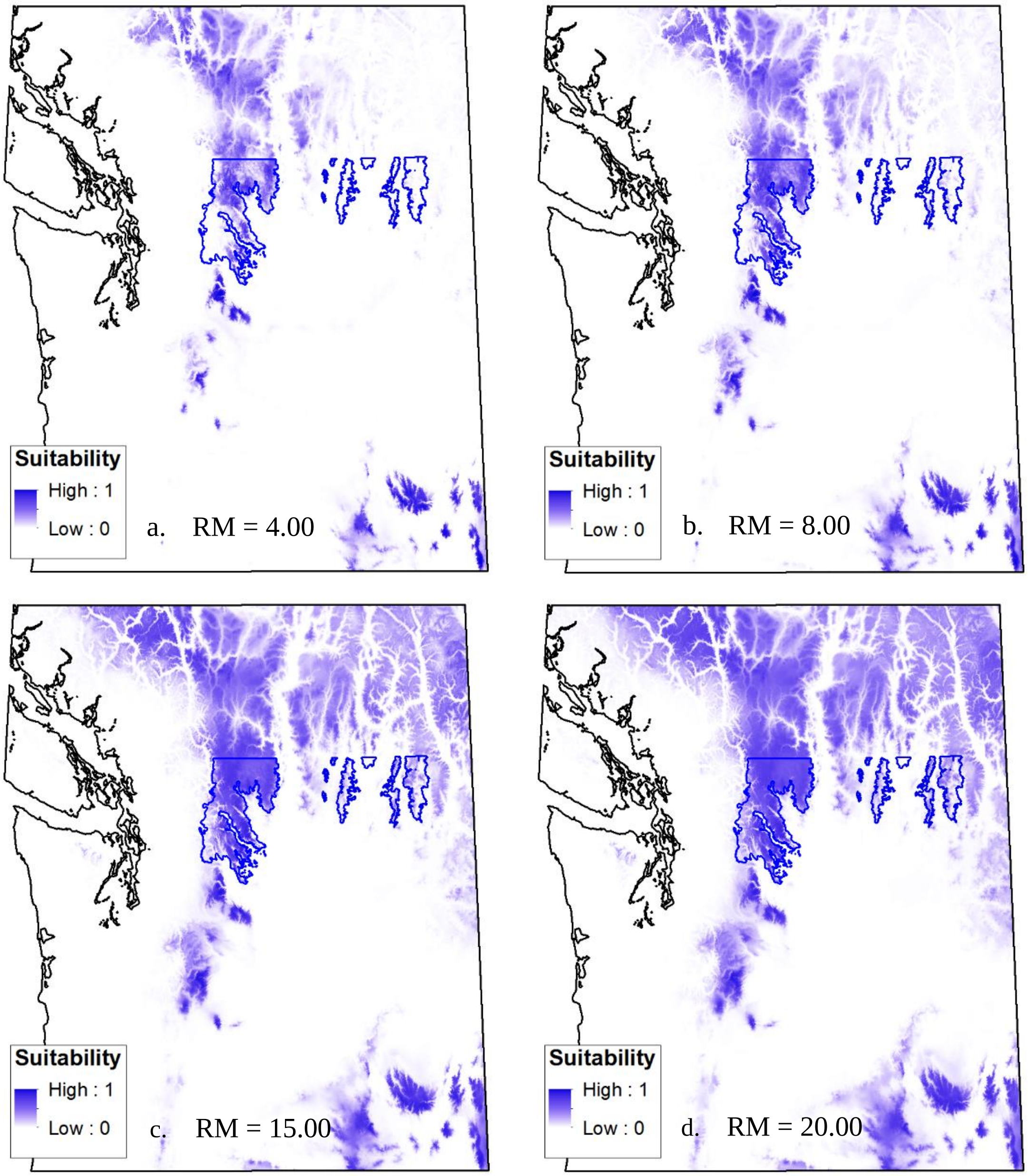


Figure 2.7. Comparison of MAXENT model projections for present-day *Lynx canadensis* habitat suitability using model type 1, showing the impact of varying the regularization multiplier (RM): (a) RM = 4.00, (b) RM = 8.00, (c) RM = 15.00, and (d) RM = 20.00. Model type 1 used the full predictor set, dropped constraining predictors, and used the full background extent (**Table 2.2**). Projections are averaged across the 10 iterations of cross-validation for each RM value. Lynx Management Zones (LMZs) are contained within blue polygons. Note that within LMZs, projections done with a RM value less than 15.00 (panels *a* and *b*), the point at which the measures of fit appear to level out, appear overfit to the areas of training data, with suitability concentrated over the presence locations and low elsewhere within LMZs. Projections from model type 2 (i.e. constrained background extent) are similar and are not shown. Suitability shown is logistic relative probability of suitability.

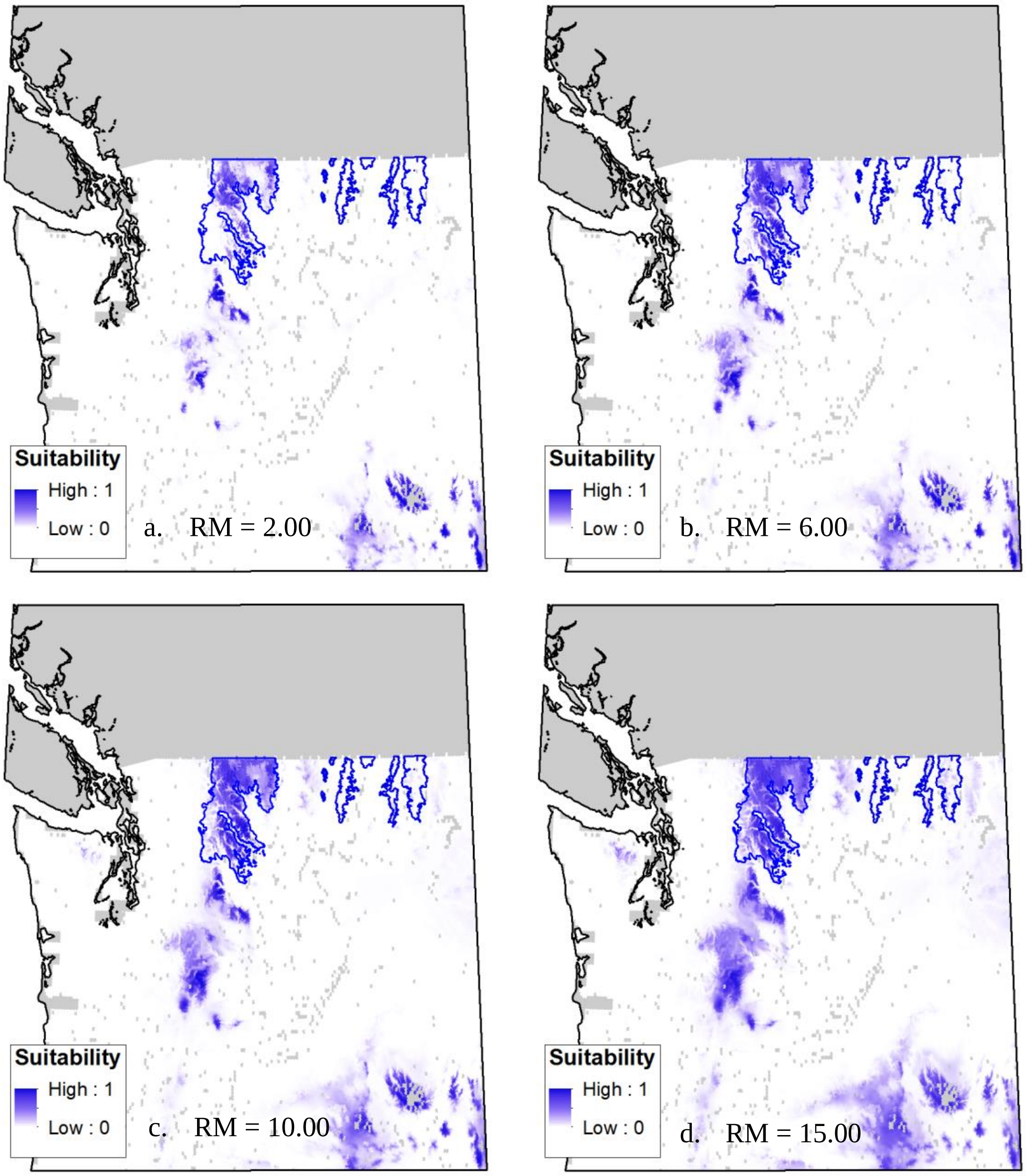


Figure 2.8. Comparison of MAXENT model projections for present-day *Lynx canadensis* habitat suitability using model type 3, showing the impact of varying the regularization multiplier (RM): (a) RM = 2.00, (b) RM = 6.00, (c) RM = 10.00, and (d) RM = 15.00. Model type 3 used the full predictor set, including the constraining predictors, and used the constrained background extent (**Table 2.2**). Projections are averaged across the 10 iterations of cross-validation for each RM value. Lynx Management Zones (LMZs) are contained within blue polygons. Note that within LMZs, projections done with a RM value less than 10.00 (panels *a* and *b*), the point at which the measures of fit appear to level out, appear overfit to the areas of training data, with suitability concentrated over the presence locations and low elsewhere within LMZs. The use of the three constraining predictors (i.e. 30-year maximum burn severity, April 1 snow water equivalent, and vegetation type) result in grid cells that lack predictions and restriction of the projection to south of the Washington-British Columbia border. Suitability shown is logistic relative probability of suitability.

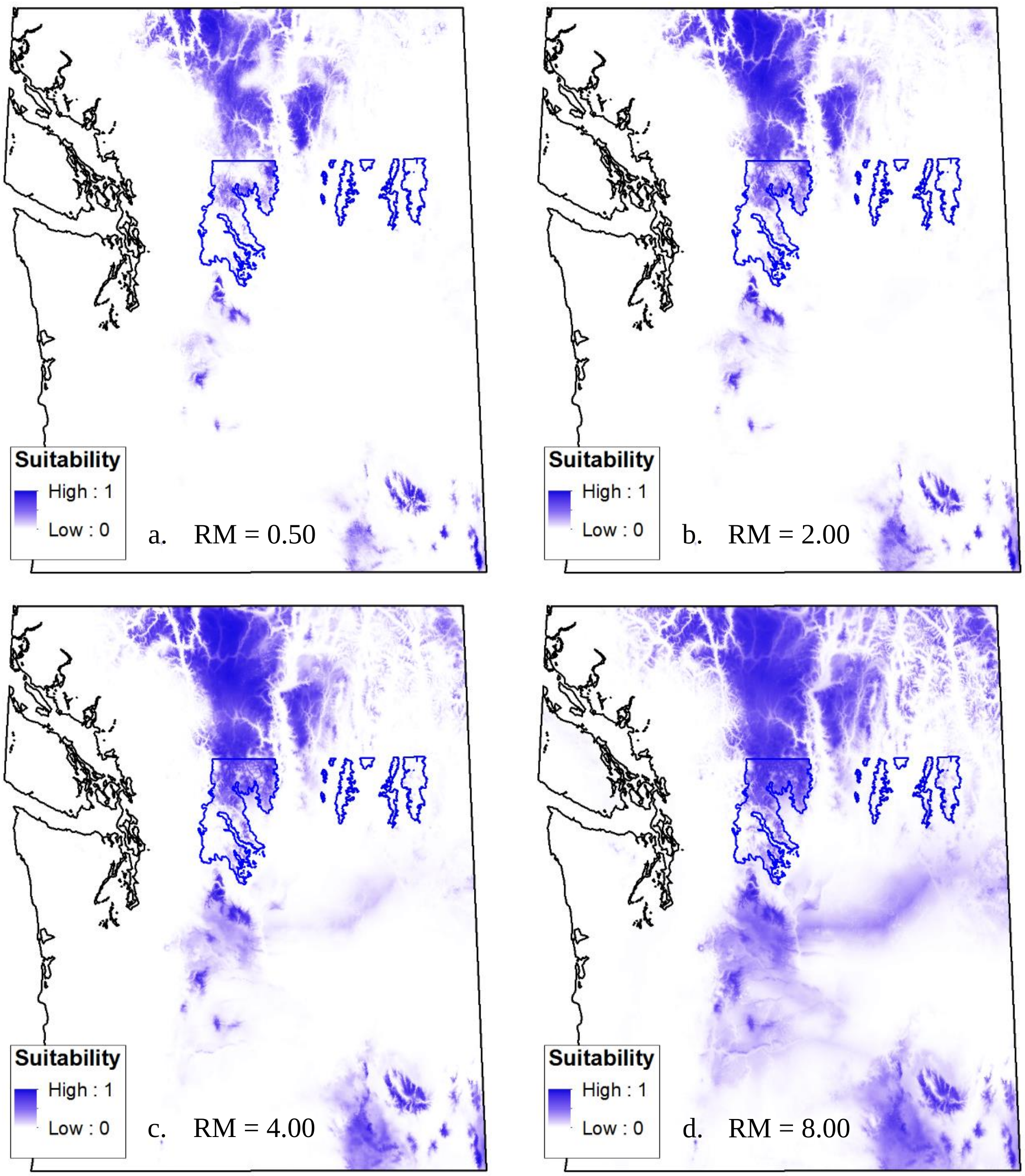


Figure 2.9. Comparison of MAXENT model projections for present-day *Lynx canadensis* habitat suitability using model type 4, showing the impact of varying the regularization multiplier (RM): (a) RM = 0.50, (b) RM = 2.00, (c) RM = 4.00, and (d) RM = 8.00. Model type 4 used the proximal predictor set, dropped constraining predictors, and used the full background extent (**Table 2.2**). Projections are averaged across the 10 iterations of cross-validation for each RM value. Lynx Management Zones (LMZs) are contained within blue polygons. Note that within LMZs, projections done with a RM value less than 4.00 (panels *a* and *b*) appear overfit to the areas of training data, with suitability concentrated over the presence locations and low elsewhere within LMZs. Consequently, although measures of fit appear to level out near a RM of 2.00, 4.00 was selected instead. Projections from model type 5 (i.e. constrained background extent) are similar and are not shown. Suitability shown is logistic relative probability of suitability.

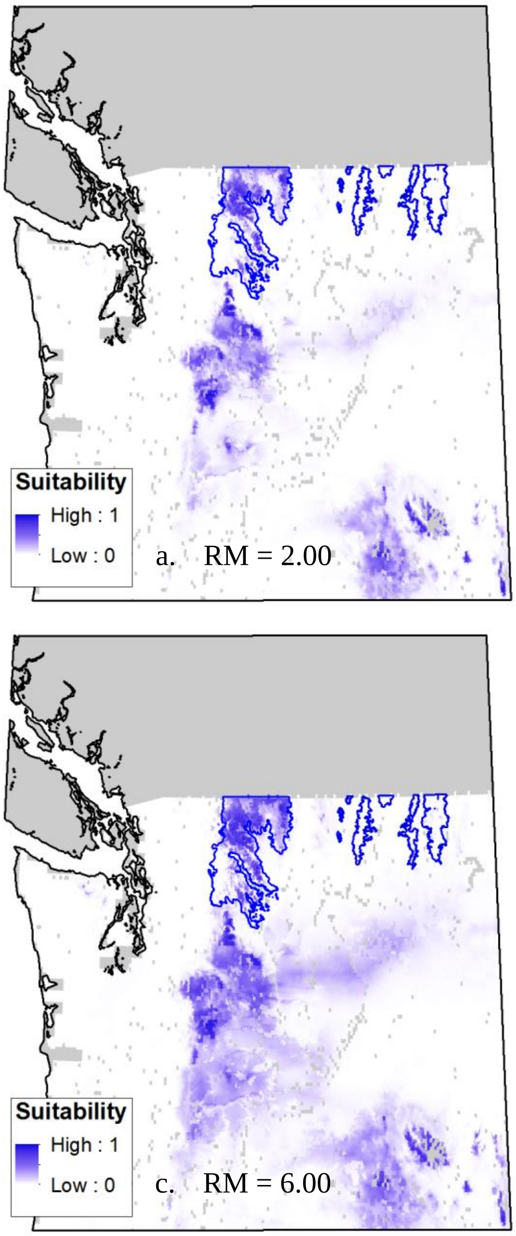


Figure 2.10. Comparison of MAXENT model projections for present-day *Lynx canadensis* habitat suitability using model type 6, showing the impact of varying the regularization multiplier (RM): (a) RM = 2.00, (b) RM = 4.00, (c) RM = 6.00, and (d) RM = 10.00. Model type 6 used the proximal predictor set, included the constraining predictors, and used the constrained background extent (**Table 2.2**). Projections are averaged across the 10 iterations of cross-validation for each RM value. Lynx Management Zones (LMZs) are contained within blue polygons. Note that within LMZs, projections done with a RM value less than 6.00 (panels *a* and *b*), the point at which the measures of fit appear to level out, appear overfit to the areas of training data, with suitability concentrated over the presence locations and low elsewhere within LMZs. The use of the three constraining predictors (i.e. 30-year maximum burn severity, April 1 snow water equivalent, and vegetation type) result in grid cells that lack predictions and restriction of the projection to south of the Washington-British Columbia border. Suitability shown is logistic relative probability of suitability.

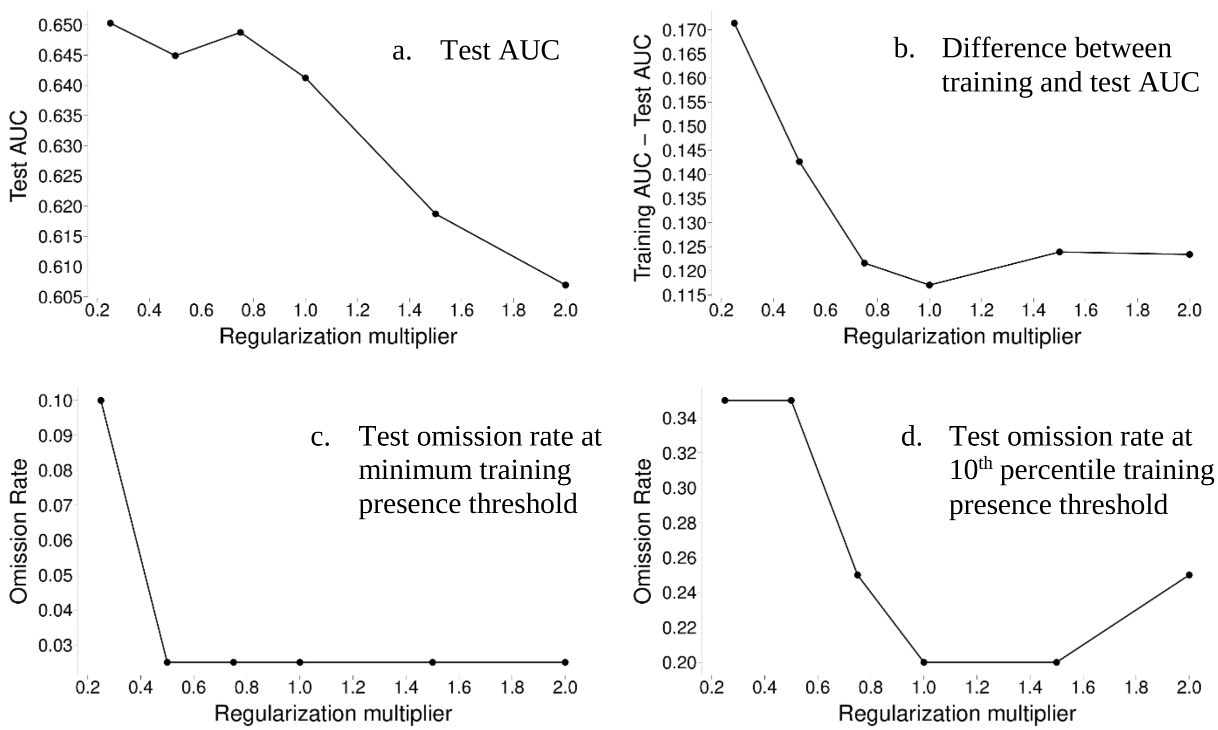


Figure 2.11. The results of the regularization multiplier tuning exercise for the *Lynx canadensis* travel-habitat model, showing threshold-independent and threshold-dependent measures: (a) test area under the curve (AUC) (b) difference between training and test AUC, (c) test omission rate at the minimum training presence threshold, and (d) test omission rate at the 10th percentile training presence threshold. Values are averaged across the 10 iterations of cross-validation of each model with a different regularization multiplier (RM) value. The travel-habitat model tuning is based only on model type 4. Test AUC refers to the discriminatory ability of the model at each RM value. Unlike with the core-habitat models, AUC values are not inflated. The other three measures characterize overfitting with lower values indicating improved generalizability, and possibly, underfitting.

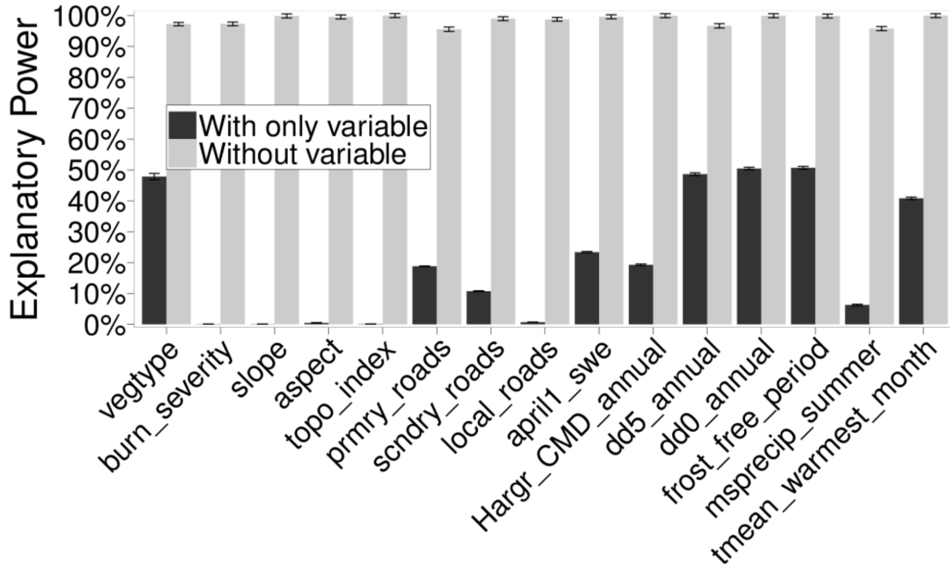


Figure 2.12. Averaged predictor jackknife for proximal model type 6 showing single-predictor importance of all variables. Model type 6 used the proximal predictor set, included the constraining predictors, and used the constrained background extent (**Table 2.2**). Predictor jackknife was averaged across the n = 200 modeled subsamples. Black bars represent standalone explanatory power of predictors and are based on the percentage of the original model's training gain achieved by the predictor in isolation. Gray bars represent explanatory power of the model when only that predictor is removed and are measured as the percentage of total training gain achieved when the predictor is excluded. Error bars represent 95% confidence intervals around the mean.

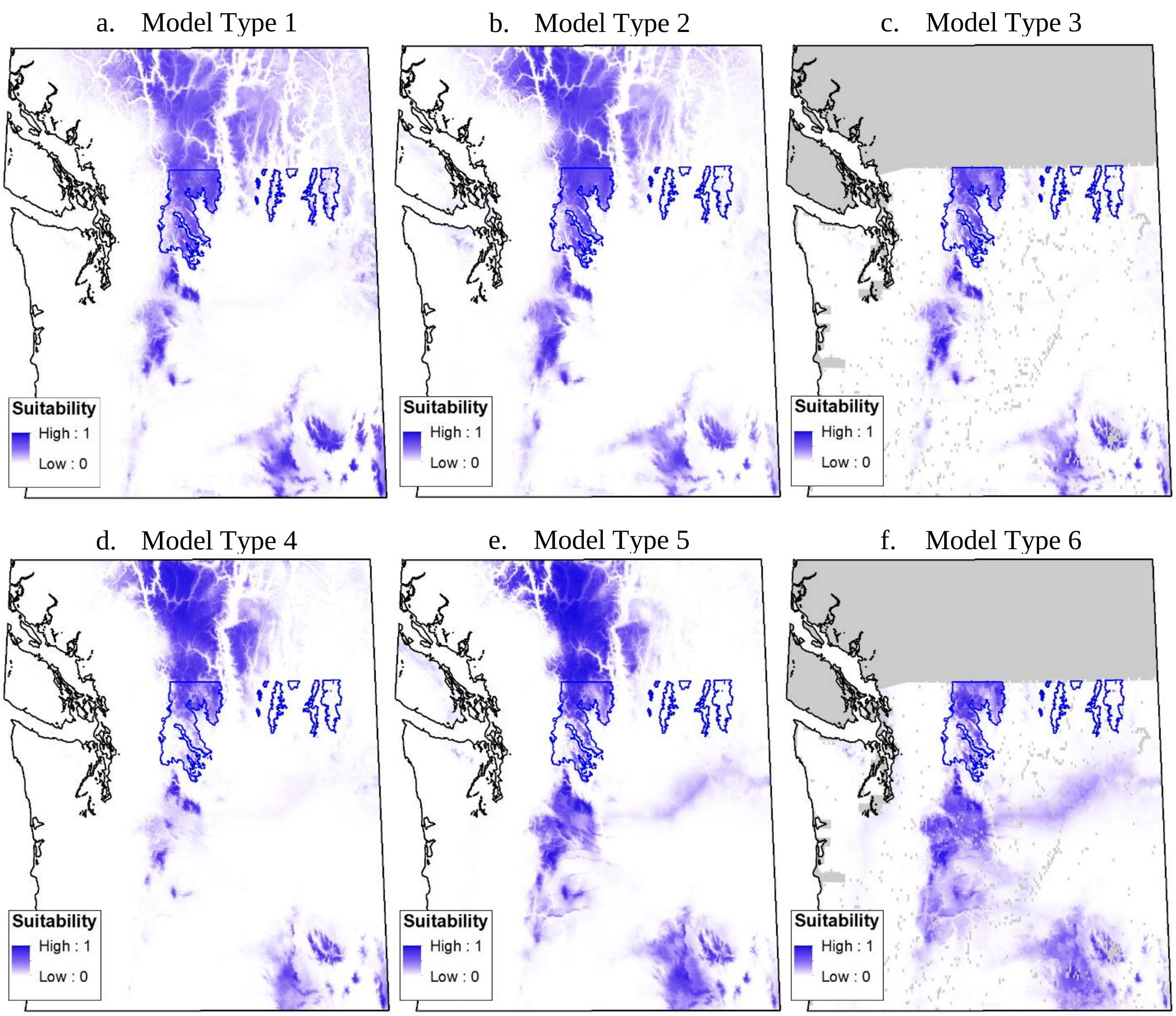


Figure 2.13. MAXENT projections for all six tuned *Lynx canadensis* core-habitat models. Lynx Management Zones (LMZs) are contained within blue polygons. Projections are averaged across the n = 200 modeled subsamples. See **Table 2.2** for a summary of the modeling approaches associated with each model type. Suitability is measured in terms of the default output from MAXENT: logistic relative probability of suitability.

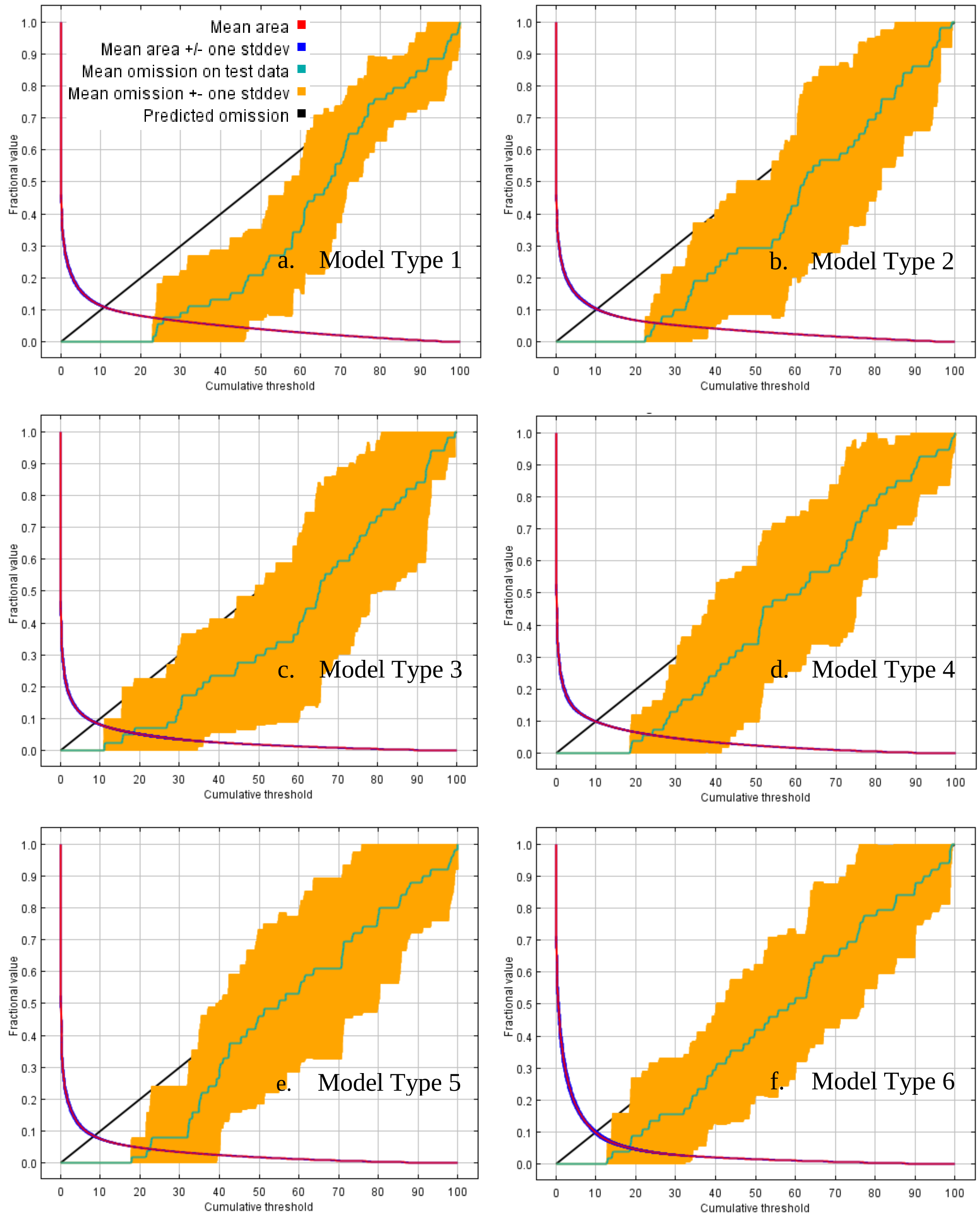


Figure 2.14. Average omission rate and predicted area for six tuned *Lynx canadensis* core-habitat model types. See **Table 2.2** for a summary of the modeling approaches associated with each model type. For each model, values are averaged across the 10 iterations of cross-validation. The c*umulative threshold* defines the cumulative suitability value at which the projection is split into a binary surface. *Fractional value* refers to either (1) the fraction of the test data omitted (i.e. omission rate) or (2) the fractional predicted area at a given cumulative threshold. Proximity of the omission rate on test data to the expected omission rate (i.e. the 1 to 1 line) indicates a good fit.

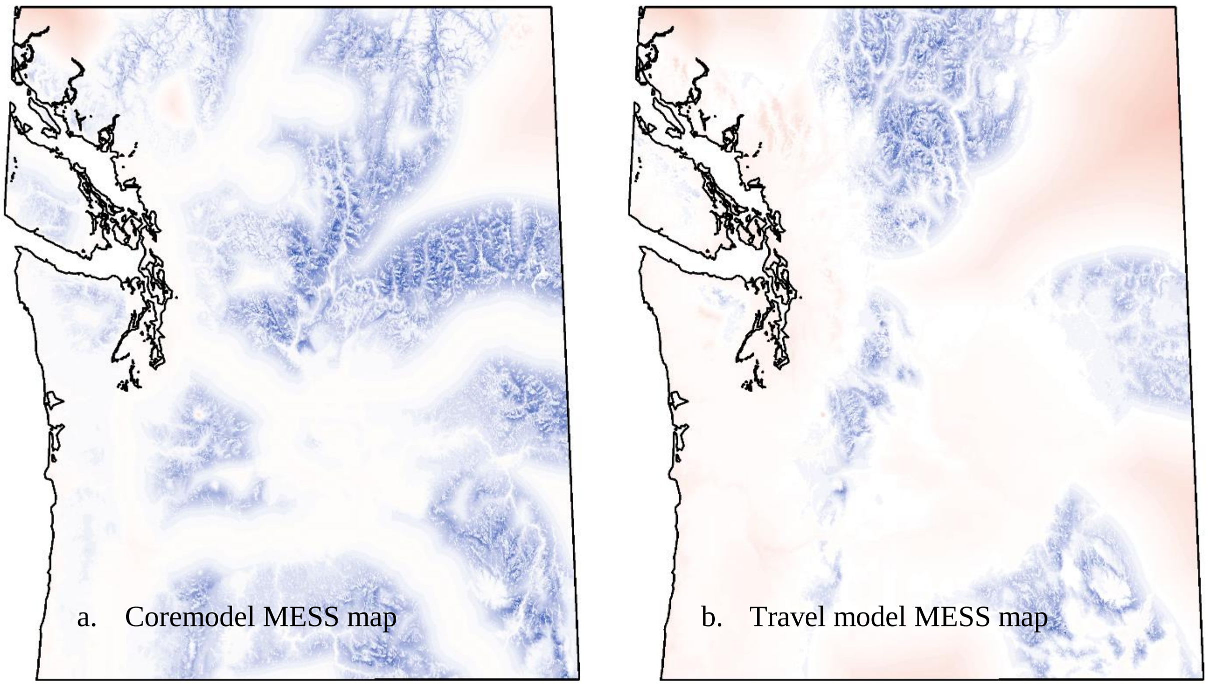
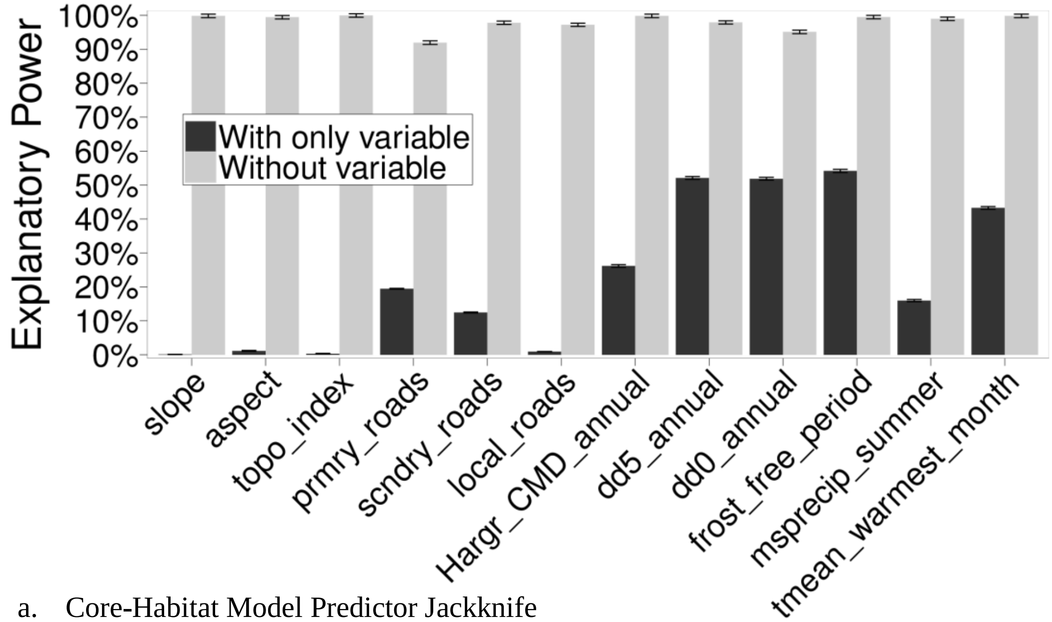
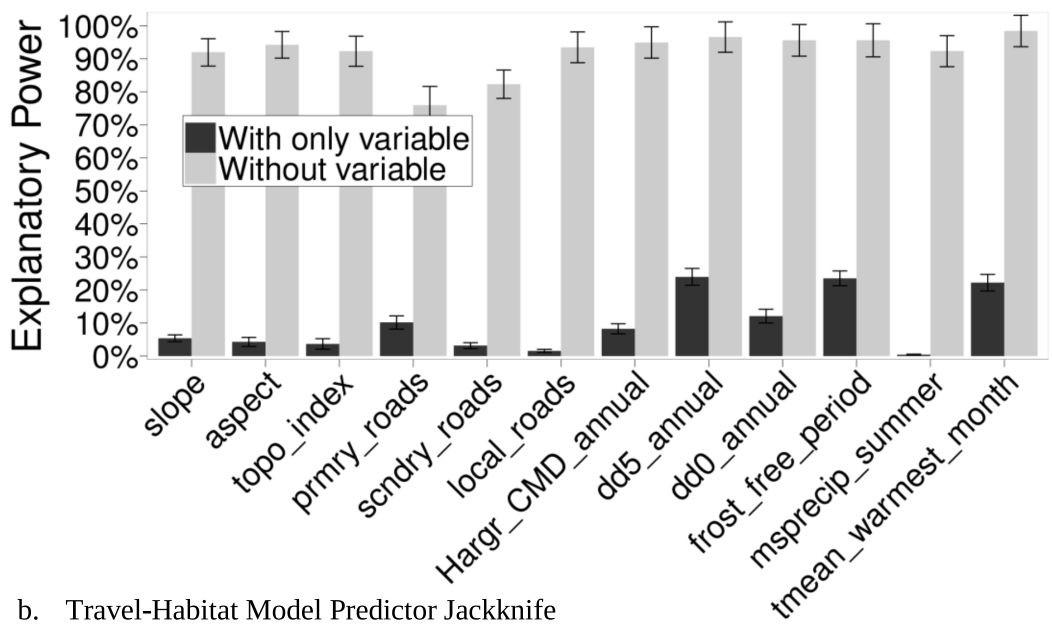


Figure 2.15. Multivariate environmental similarity surface (MESS) maps for the *Lynx canadensis* core-habitat and travel-habitat models. Positive values (blue) reflect low to no environmental novelty. Negative values (red) reflect environmental novelty. Zero values (white) indicate that values are different than median training space values, but that values are not outside the range. More intense colors indicate greater magnitude. Maps are provided on the same scale (80 to -800). MESS maps are averaged across the number of subsamples used for the models (core: n = 200, travel: n = 10).



a. Core-Habitat Model Predictor Jackknife



b. Travel-Habitat Model Predictor Jackknife

Figure 2.16. Averaged predictor jackknife showing single-predictor importance of all variables for final *Lynx canadensis* habitat models: (a) the core-habitat models and (b) the travel-habitat models. For core habitat, the predictor jackknife was averaged across the n = 200 modeled subsamples, whereas for travel habitat, the predictor jackknife was averaged across the n = 10 modeled subsamples. Black bars represent standalone explanatory power of predictors and are based on the percentage of the original model's training gain achieved by the predictor in isolation. Gray bars represent explanatory power of the model when only that predictor is removed and are measured as the percentage of total training gain achieved when the predictor is excluded. Error bars represent 95% confidence intervals around the mean.

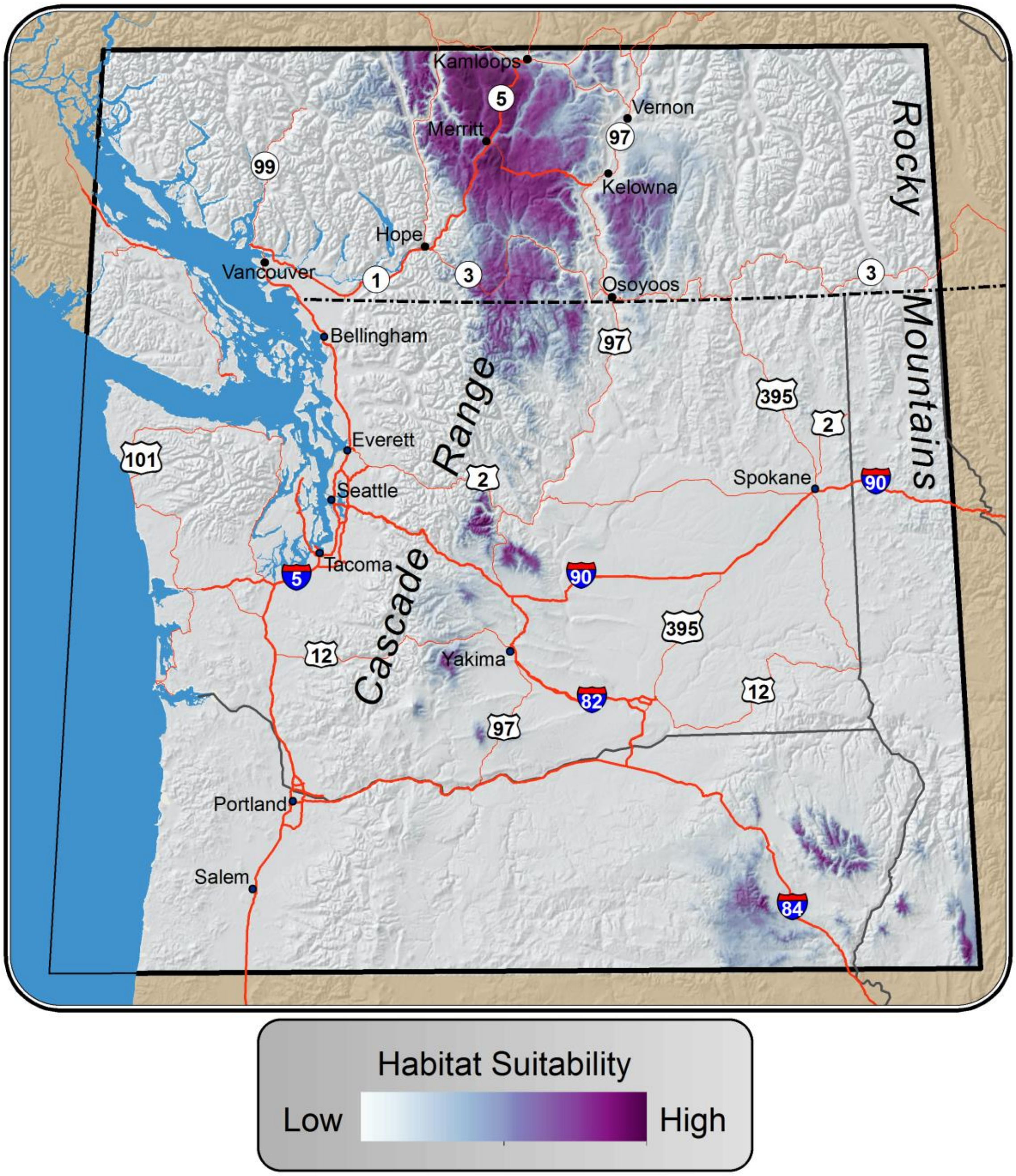


Figure 2.17. MAXENT projection map showing relative suitability of *Lynx canadensis* core habitat based on the final core-habitat model. Projection is averaged across the n = 200 modeled subsamples. Suitability is measured in terms of the default output from MAXENT: logistic relative probability of suitability.

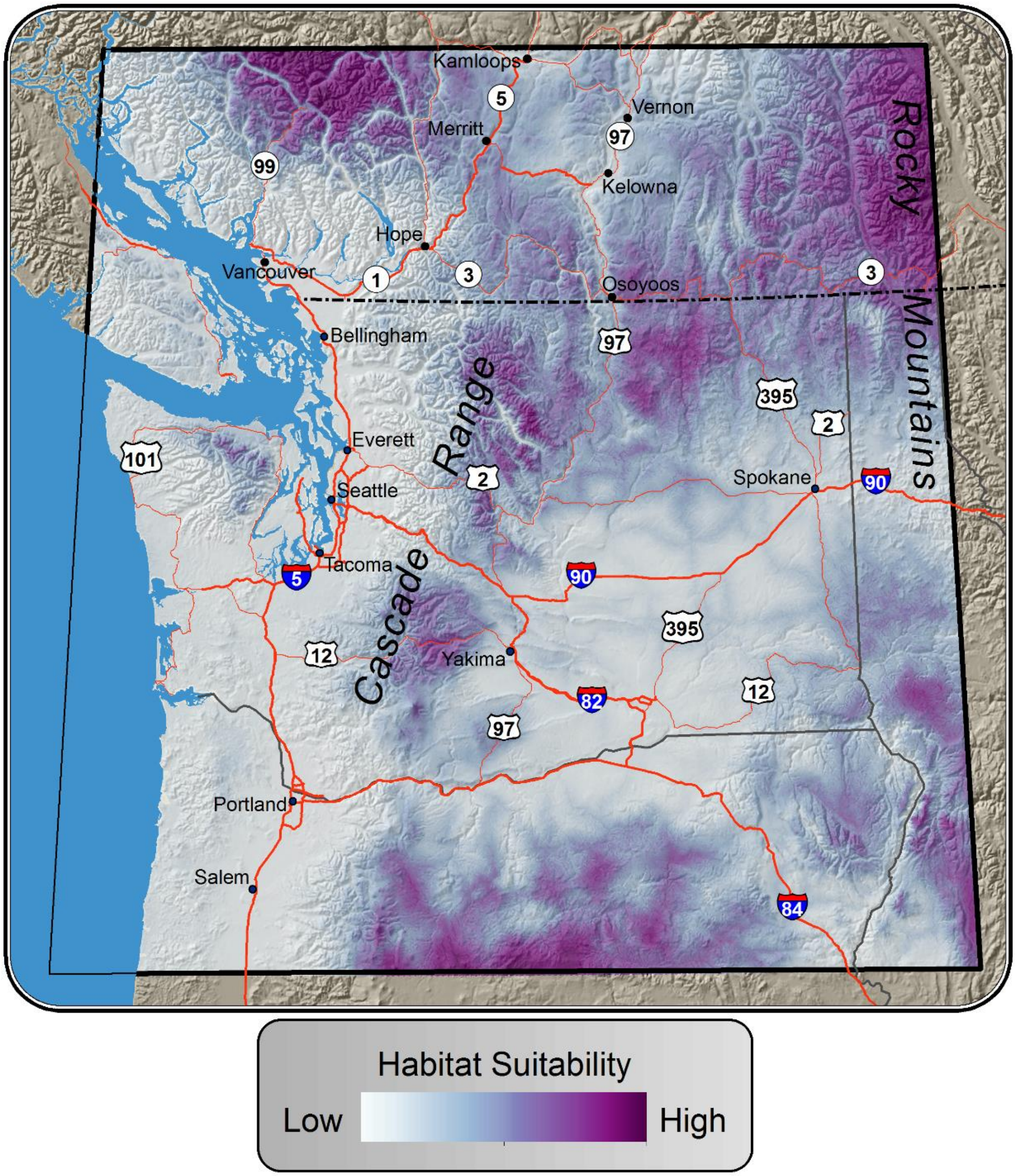


Figure 2.18. MAXENT projection map showing relative suitability of *Lynx canadensis* travel habitat. Note that travel habitat is projected to be far more abundant than core habitat. Projection is averaged across the n = 10 modeled subsamples. Suitability is measured in terms of the default output from MAXENT: logistic relative probability of suitability.

CHAPTER 3. HABITAT SUITABILITY PROJECTIONS FOR CANADA LYNX IN THE WASHINGTON-BRITISH COLUMBIA TRANSBOUNDARY REGION

Abstract

I used MAXENT to project regional-scale, transboundary core-habitat suitability models for lynx in the Washington-British Columbia (BC) transboundary region to eighteen future climates projected for three future time periods (2020s, 2050s, and 2080s), two Representative Concentration Pathways (RCPs; 4.5 and 8.5), and three downscaled Coupled Model Intercomparison Project Phase 5 (CMIP5) models (CanESM2, CNRM-CM5, and CCSM4). I evaluated and compared outcomes using analysis of projected core-habitat and range-area metrics and visual assessment of projection maps to identify the most likely impacts of climate change on regional pattern, location, quality, and extent of potential habitat suitability through time. Projections for future climates unanimously indicated a northward range shift and increased habitat fragmentation over time. Although results support previous broad-scale and regional studies suggesting range losses for lynx throughout the southern periphery in response to climate change, they also indicate much higher rates of change. Outcomes were highly variable, but all scenarios predicted loss of all suitable habitat cores in the Okanogan Lynx Management Zone (LMZ) by the 2050s, and most predicted loss of all cores within the study area by the 2080s. Impacts were more extreme for the global climate model (GCM) and RCP with the highest temperature anomaly, CanESM2 RCP 8.5. Higher confidence in projections, based on lower environmental novelty, was associated with areas where suitable cores were predicted. For lynx in the Washington-BC transboundary region, these results advance our understanding of potential futures, delineate potential outcomes at a finer-resolution than any

previous analyses, call attention to the need to evaluate region-specific outcomes based on unique regional habitat-selection drivers, and characterize uncertainties so that managers can contextualize likely changes.

Introduction

As a species threatened in the contiguous U.S. that is dependent on climate-sensitive landscape conditions, Canada lynx (*Lynx canadensis*) are vulnerable to climate change at southern range peripheries, especially in light of recent fires that have consumed a significant portion of suitable lynx habitat. An uncertain climate future is one of the many challenges for Canada lynx (*Lynx canadensis*) management in Washington State, with climate change identified as an anthropogenic influence that can negatively impact Canada lynx (hereafter "lynx") and lynx habitat (Interagency Lynx Biology Team 2013). As a threatened species both federally in the U.S. and locally in Washington State, lynx are dependent on environmental conditions that are sensitive to climate. These include snowpack persistence, depth, and firmness, as mediated by temperature and freeze-thaw dynamics, and vegetative community structure and horizontal cover, as mediated by temperature, climatic moisture deficit, summer precipitation, frost-free period, and growing degree days (see *Chapter 2*). To complicate matters, lynx in Washington State are at the southern margin of their North American range where vulnerability to climate impacts is expected to be most extreme (Anderson et al. 2009) and there is some evidence that contractions to lynx range have already occurred (Laliberte and Ripple 2004, Bayne et al. 2008).

The 2006 Tripod fire significantly reduced already fragmented habitat within the Okanogan Lynx Management Zone (LMZ) (Koehler et al. 2008). Although these impacts might otherwise be temporary until vegetation can reestablish in the next 10-40 years (Interagency Lynx Biology

Team 2013), it is unknown whether habitat there or in the surrounding areas will continue to be suitable, and if so, to what degree and where. Wildfires can reset the physical environment and can change vegetative communities, especially where climate has already shifted in favor of new communities (Frelich and Reich 1995, Agee 2000, Soja et al. 2007, Higuera et al. 2009). Projected and observed climate-induced changes to snow conditions (Hamlet and Lettenmaier 1999, McKelvey et al. 2011), fire regimes (Rogers et al. 2011, Sheehan et al. 2015), bioclimatic envelopes for vegetation and vegetation compositions (Soja et al. 2007, Littell et al. 2010, Coops et al. 2011, Sheehan et al. 2015), forest productivity (Raymond and McKenzie 2012), and other environmental conditions contingent upon climate necessitate a fuller understanding of potential outcomes than is currently available.

No studies to date have projected and evaluated potential lynx habitat at a regional scale for Washington State under future climate scenarios to examine how Washington lynx are likely to respond to climate change, nor evaluated uncertainty in the possible impacts of climate change on Washington lynx habitat. It is currently unknown whether Washington State can continue to support lynx populations in the future, and if so, to what degree and where. Broad-scale projections of lynx range (Carroll 2007, Gonzalez et al. 2007, Peers et al. 2014), are often based on small and limited-occurrence datasets or coarse-grained methods that are frequently too imprecise to apply results to regional-scales such as those needed for the Washington-BC transboundary region. Broad-scale models also combine highly variable drivers of lynx habitat suitability, derived from lynx habitats throughout the U.S., into a one-size-fits-all outcome. Although useful for predicting likely broad-scale outcomes, these projections are limited with respect to conservation applications at smaller scales, such as needed for Washington State lynx populations.

Much uncertainty is involved in modeling the impacts of climate change on lynx and lynx habitat because of variability in climate projections. Although uncertainty has been identified as a complicating factor in planning for lynx conservation (Murray et al. 2008, Interagency Lynx Biology Team 2013), uncertainty with respect to the impacts of climate change on lynx habitat suitability has not been evaluated for Washington State. Beginning with Special Report on Emissions Scenarios (SRES) or Representative Concentration Pathway (RCP) scenarios, variability within model possible forcings is large (Glick et al. 2011). That uncertainty begins to expand as these emission or concentration scenarios are incorporated into highly complex and imperfect global climate models (GCMs), of which there are many (Glick et al. 2011). What is needed is to understand the wide range of outcomes possible for lynx given the variation in future climate spaces.

Previous Broad-Scale Projections for Canada lynx

Several broader-scale studies have projected lynx distribution or population change for different time periods in the next century (Carroll 2007, Gonzalez et al. 2007, Peers et al. 2014). To evaluate potential changes in regional lynx populations in southeastern Canada and the northeastern U.S. by 2055, Carroll (2007) used a spatially explicit population model based in part on relationships to predicted changes in snowfall and vegetation derived from a broad-scale study by Hoving et al. (2005). Carroll (2007) predicted that changes in snowfall simulated by the intermediate to high climate change scenario (A2) and the Parallel Climate Model reduced modeled range margin lynx populations in this region by 59%.

Gonzalez et al. (2007) analyzed reliance of lynx on snow cover in the U.S. and Canada using occurrence data and projected lynx distribution and changes therein based on boreal forest and projections of suitable snowfall, using a range of Intergovernmental Panel on Climate Change

(IPCC) climate scenarios and MC1 dynamic global vegetation model (DGVM) projections. They found that broad-scale changes in areas that receive continuous snow cover for four months out of the year and changes in the distribution of boreal forests may shift lynx habitat northward by up to 200 km and decrease potential habitat by up to two thirds within the contiguous U.S. and by up to one fifth across the continental U.S. and Canada combined by 2100. Among their list of vulnerable areas were the Okanogan and Wenatchee National Forests of Washington State.

Peers et al. (2014) used MAXENT (Phillips et al. 2006) in combination with screened museum occurrence data to model and compare the bioclimatic niche over the southern range (i.e. the most southerly 300 km of the present range) of lynx for the present day, 2050, and 2080. They used climatic data from WorldClim for the A2 and B1 emission scenarios under the CGCM3 model and under the CSIRO mk3.5 model. They then assessed whether adding projections of prey distributions to lynx projections might further restrict the range of lynx. For the climate only models, they projected a 29.14% reduction for 2050 and a 50.98% reduction for 2080 within the southern range under the A2 emissions scenario. In models that included prey distributions, additional range reductions in the southern periphery were between 0.56% and 66.1% for 2050 and between 0.036% and 61.0% for 2080, with the low-end values corresponding to an assumption that lynx can adapt by increasing their reliance on red squirrels (*Tamiasciurus hudsonicus*) as a prey species.

Objectives and Expectations

For lynx in the Washington-British Columbia (BC) transboundary region, my first objective was to quantify and describe the average projected impacts of climate change on regional pattern, location, quality, and extent of potential habitat through time. My second objective was to expand on this concept by quantifying and demonstrating the range of possible outcomes with respect to these same metrics across time periods and climate scenarios, while identifying areas of greatest and least uncertainty. To address these objectives, I used MAXENT to project the core-habitat model developed in *Chapter 2* to eighteen different climate futures, characterized by projections of environmental and climate data for three future time periods, two emission pathways, and three Coupled Model Intercomparison Project Phase 5 (CMIP5) models. Based on suitability thresholds estimated objectively, I then mapped core and range areas in all time periods and scenarios, evaluating and comparing the associated metrics. I explored the progression of change across the three time periods using these metrics along with visual assessment of projections and quantified the range of variability in outcomes across climate futures. I also evaluated indications of shifts in the southern range margin of the lynx distribution, focusing on changes in suitability within LMZs and lynx critical habitat. Finally, I explored factors that may change outcomes, evaluated the implications of outcomes for conservation applications, and identified areas where additional research is needed.

I expected to find that the majority of projections show increased fragmentation of core habitats with time, with reductions in average size and quality of the most suitable habitats, especially at the southern edge of currently suitable habitat. I also expected to see substantial northward shifts in the margin of lynx habitat. I expected these results to be more extreme for RCP 8.5 than for RCP 4.5 and more extreme for the GCM with the highest temperature anomaly due to the dependence of the final core model on temperature-driven predictors (see *Chapter 2*). I expected that habitat suitability would vary widely among climate scenarios and time periods, with the biggest differences at any given time period arising from differing emission pathways.

Materials and Methods

MAXENT Modeling

Chapter 2 provides an in-depth discussion of the MAXENT settings used (e.g. feature classes and regularization) and modeling process, including preparation and subsampling of the occurrence data, model tuning and selection, selection of background extents used to define available habitat for the final core-habitat model, and evaluation of model-fit metrics and predictor importance. The final core-habitat model was trained using a set of prescreened predictors referred to as the proximal predictor set (**Table 3.1**), a partially masked background extent defined as a 100-km buffer around all presence locations, and 200 spatially rarefied subsamples. The core-habitat model required adjustment of the default regularization parameter to establish a balance between model fit and complexity. Predictors that constrained projections south of the BC border (i.e. April 1 Snow Water Equivalent, modal MC2 potential vegetation type, and maximum burn severity) were dropped following an evaluation of model performance with and without these predictors.

To obtain the maximum variability in habitat suitability between occurrence data subsamples, I projected models to each of the 18 climate futures for all core-habitat subsamples (n = 200). As was done for present-day habitat suitability projections, clamping of response curves to within the range of the predictor values was turned off in MAXENT for all projections. Multivariate environmental similarity surface (MESS) analysis was performed for all projections. MESS maps depict differences between the environment used to train each model and the environment to which the model is projected by measuring the similarity of each grid cell to the reference grid cells used in the analysis (Elith et al. 2011). MAXENT's default logistic output was used to define relative probability of suitability across the study area, with the assumption that habitat selection is equivalent to habitat suitability. The trained MaxEnt models were projected to the entire study area (**Figure 2.1**). For a review of the application of MaxEnt to species distribution modeling, see *Chapter 2*.

Environmental Predictors

Predictors included in the core-habitat model are provided in **Table 3.1** and were selected based their relationship with previously studied drivers of lynx habitat selection. To achieve projections into climate futures, topographic variables (i.e. slope, aspect, and compound topographic index) and distance to road variables were held constant, whereas climatic variables from ClimateWNA (Wang et al. 2012) were updated depending on the scenario. *Appendix B* describes the preparation of these updated climatic predictors as well as the other predictors included in the model.

Because downscaled projections from climate models are uncertain, I used multiple climate models and emission scenarios to capture the range of impacts and to explore uncertainties between these pathways (Glick et al. 2011). For this analysis, I used downscaled climate data from GCMs participating in the World Climate Research Programme's CMIP5 (Rupp et al. 2013). In selecting global model CO_2 emission forcing, I chose RCP 4.5, based on the assumption of moderate climate action, and RCP 8.5, based on the assumption of no climate policy and business-as-usual emissions.

Projections were produced for three future climates characterized by 30-year climatic averages: 2020s (2010-2039), 2050s (2040-2069), and 2080s (2070-2099). For each time period, I projected habitat suitability for the two RCPs from three GCMs: CanESM2, CNRM-CM5, and CCSM4. These three models are among the best eleven out of forty-one models in terms of relative error of ensemble means for a variety of performance criteria when compared to observational records (Rupp et al. 2013). These models were selected from those eleven models to capture the range of projected changes in both temperature and precipitation, which can be viewed using the Integrated Scenarios Project visualization tools (http://climate.nkn.uidaho.edu/IntegratedScenarios/gallery_vis.php). Generally, models represent high, medium, and low changes in annual temperature while also capturing a range of possibilities for precipitation changes, including increases and decreases in some cases. However, note that most of climate scenarios predicted increases rather than decreases in precipitation. For this study, within the general area of the Okanogan LMZ, CCSM4 generally represents the low end of possible temperature increase for models within each RCP, whereas CNRM-CM5 generally represents medium temperature increase, and CanESM2 generally represents high temperature increase. Precipitation changes depend on time period and RCP for each model but cover the range of possibilities, including varying between increasing and decreasing in the 2020s, ranging from low (CanESM2) to medium (CCSM4 and CNRM-CM5) increases in the 2050s, and ranging from low (CanESM2) to high (CNRM-CM5) increases in the 2080s.

Table 3.1. Importance of predictors in the final *Lynx canadensis* core-habitat suitability model

Jackknife Importance * (% Explanatory Power)	Predictor Name
1 (54.2 %)	frost-free period
2 (52.1 %)	degree-days above 5°C (growing degree-days)
3 (51.9 %)	degree-days below 0°C (chilling degree-days)
4 (43.3 %)	mean warmest month temperature (°C)
5 (26.2%)	Hargreaves climatic moisture deficit (mm)
6 (19.5%)	Distance to Primary Roads (m)
7 (16.0 %)	mean annual summer (May to Sept.) precipitation (mm)
8 (12.4%)	Distance to Secondary Roads (m)
(< 2 %)	Aspect
(< 2 %)	Compound Topographic Index
(< 2 %)	Slope (°)
(< 2 %)	Distance to Local Roads (m)

* Jackknife importance alludes to the percentage of explanatory power each predictor had when it was the only predictor in the model compared to the explanatory power of the model containing all predictors. See *Chapter 2* for additional information on the core-habitat suitability model.

Evaluation of Projections

I averaged model projections and MESS maps across all core habitat subsamples (n = 200). First, I applied a threshold suitability value of 0.38 to predictions of suitable lynx habitat to construct binary depictions of the range of lynx within the study area. This threshold suitability value is equal to the equal training sensitivity and specificity logistic threshold, at which positive and negative presence observations have equal chance of being correctly predicted (Freeman and Moisen 2008). Next, I used the Core Mapper tool in the ArcGIS Gnarly Landscape Utilities toolbox (version 2.0) (Shirk and McRae 2013) in ArcGIS 10.3 to identify habitat concentration areas using specific thresholding techniques that converted the continuous maps of habitat suitability to binary depictions of core-habitat areas.

Core Mapper performs a moving window analysis and then uses a threshold minimum average habitat value to identify core patches of suitable habitat. It then removes pixels within each binary core patch that themselves fall beneath a minimum per-pixel threshold value. Cores that do not meet a minimum area are also removed. Finally, this tool also calculates the area and the average suitability value of each core. I used a moving window radius of 5.29 km, which corresponds to the most recent estimate of the average lynx range size in the North Cascades (88 km^2; Vanbianchi 2015). For the minimum threshold average habitat value, I again selected 0.38. I allowed pixels with suitability values less than 0.27, the minimum training presence logistic threshold, to be excluded. The minimum training presence logistic threshold is the suitability threshold below which no training presences are predicted. Resulting cores less than 100 km^2 were considered too small to constitute a core. This 100 km^2 values is roughly consistent with previous estimates of lynx densities in the North Cascades of 2.3 lynx / 100 km^2 (Koehler

1990a). Core Mapper outputs include core polygons in addition to the area and average suitability of each core.

Using the results of core mapping, I calculated the average number, total and per core area, and suitability of all core habitats and the percentage change in each between present and future projections across all time periods and scenarios. I also quantified the range area in each binary projection and calculated the percentage change. I then aggregated these statistics within different time periods, CMIP5 models, and RCPs. I mapped core areas and overall suitability for each projection. I used these core-habitat statistics with visual assessment of suitability maps to evaluate and rank core-habitat projections based on area and suitability, identify commonalities between projections, and describe and quantify likely changes to habitat. I considered number of cores and total core area to be primary in describing changes to core habitat and considered per core area and suitability to be secondary. I relied on projection maps to describe the direction of range change and to identify changes in the location and distribution of cores. I used range reduction statistics to characterize and rank uncertainty in outcomes between different time periods under different climate scenarios and used MESS maps to depict environmental novelty within the study area for each climate scenario. Finally, I assessed the geographic locations of cores with respect to LMZs (Stinson 2001) and lynx critical habitat and identified key core habitats for the future.

Averaging of habitat suitability projections and MESS maps was done in RStudio using MAXENT outputs, with the help of the R package *raster* (R Core Team 2013, RStudio Team 2015, Hijmans 2016). All plots were produced and all statistics computed in RStudio using the packages *Cairo* (Urbanek and Horner 2015), *scales* (Wickham 2016), and *ggplot2* (Wickham 2009). Maps were produced in ArcGIS 10.3 (ESRI 2014).

Results

Core and Range Metrics

Within the study area, average number of cores, range area, total core area, average per core area, and average core suitability all decreased through time (**Figures 3.1a, 3.2a**, **3.3a,** and **3.3b**, **Tables 3.2** and **3.3**, **Tables C.1 - C.4**). Within the study area for the present-day (**Figure 3.7**), thirteen cores were predicted, with a total core area of 26,340 km^2, an average per core area of 2,026 km^2 (SD = 4,740) and an average suitability of 0.58 (SD = 0.06) on a scale of 0.38 to 1 (**Table 3.3**). Total range size for the present day was predicted to be 28,492 km^2 (**Table 3.3**). Total core area within Washington State and in the Okanogan LMZ was predicted to be 3,642 km^2 and 2,501 km^2 respectively. Total suitable habitat in Washington State above the binary range-area threshold was projected to be 4,091 km^2.

The best outlook for lynx in the future was the CCSM4 RCP 4.5 scenario (**Figure 3.8**), with small initial declines in all metrics and five cores persisting into the 2080s, though suffering large reductions in area and suitability. In general, the least favorable was the CanESM2 RCP 8.5 scenario (**Figure 3.9**), with the most extreme declines in all metrics overall and total loss of all cores and most range area by the 2050s. The only exceptions to this are the CNRM-CM5 RCP 4.5 and RCP 8.5 scenarios in the 2020s, with stronger reductions noticeable in the Okanogan LMZ habitats than for the corresponding CanESM2 scenarios. Otherwise, CCSM4 RCP 8.5, CNRM-CM5 RCP 4.5 and 8.5, and CanESM2 RCP 4.5 were middle of the line scenarios, but were closer in overall impact to the CanESM2 RCP 8.5 scenario than to the CCSM4 RCP 4.5 scenario (**Figures 3.1** and **3.2**, **Table 3.2**).

Starting with the 2020s, within the entire study area, total core area was reduced between 29% and 68% and number of cores was reduced between 23% and 54%, depending on the scenario (**Table 3.2**). Range area, total per core area, and suitability were also reduced throughout the study area (**Table 3.2**). The most extreme scenario at this time period, CNRM-CM5 RCP 8.5, predicted loss of all habitat within the Okanogan LMZ in the 2020s. For the remaining scenarios, the average reduction in core area was roughly 50% within the Okanogan LMZ and suitability of the remaining cores was lower. In the 2050s, within the entire study area, total core area was reduced between 82% and 100% and number of cores was reduced between 62% and 100%, depending on the scenario (**Table 3.2**). However, all scenarios predicted loss of all cores within the Okanogan LMZ by the 2050s and the most extreme scenario, CanESM2 RCP 8.5, predicted loss of all core and range areas in the study area by this time period (**Figure 3.9**, **Tables 3.2** and **3.3**). Range area, total per core area, and suitability were further reduced over the 2020s throughout the study area (**Table 3.2**).

Loss of all core and range areas was predicted by the CanESM2 RCP 4.5 scenario and all RCP 8.5 scenarios by the 2080s (**Figures 3.8** and **3.9**, **Tables 3.2** and **3.3**) and by the CanESM2 RCP 8.5 scenario by the 2050s (**Figure 3.9**, **Tables 3.2** and **3.3**). In all other scenarios, some cores were retained during these time periods. However, by the 2080s, all scenarios predicted over 98% range and core area loss, with the exception of CCSM RCP 4.5 at 88% and 91%, respectively. Cores predicted to remain in the 2080s were small ($\leq$ 462 km^2) and of marginal suitability ($\leq$ 0.50) on average.

By CMIP5 model across all RCPs and time periods, average predictions of both core numbers (**Figure 3.1b**) and total core area (**Figure 3.2b**) were highest under CCSM4, middle of the line for CNRM-CM5, and lowest under CanESM2 (**Table 3.4**). However, similar to un-aggregated metrics, aggregated metrics also indicated that outcomes for CNRM-CM5 were more similar to CanESM2 than to CCSM4. On average across all CMIP5 models and time periods, RCP 4.5 predicted less reduction than RCP 8.5 (**Figure 3.2b, Table 3.4**) for these same metrics. For core numbers and total core area, the gap between RCP 4.5 and 8.5 narrowed for the more impactful scenarios, CNRM-CM5 and CanESM2, when averaged across all time periods (**Figures 3.1b** and **3.2b**).

I did not compare aggregated statistics for per core area (**Table C.3**) and suitability (**Table C.4**) because these statistics were biased upward for higher impact scenarios due to the absence of cores under these scenarios. However, the average loss in number of cores, total core area, and range area was predicted to be higher in all time periods than declines in per core area or suitability (**Table 3.2**). When all scenarios were combined, models predicted an average 41% reduction in core number, 51% reduction in total core area, and 49% reduction in range area in the 2020s from the present-day, compared to an 18% drop in per core area and a 4% drop in suitability (**Table 3.2**). By the 2080s, a decrease of 92% in number of cores and 98% in total core area and range area was predicted, compared to 79% decrease in per core area and a 15% in suitability (**Table 3.2**).

Variability in Range Area Outcomes

Variability was minimized when outcomes were separated by time period and CMIP5 model (i.e. both RCPs combined) (**Figures 3.4a** and **3.5a**, **Table 3.5**). Variability increased minimally when outcomes were separated by time period and RCP (i.e. all CMIP5 models combined) (**Figures 3.4b** and **3.6a**, **Table 3.5**). Finally, variability increased greatly when outcomes were separated by CMIP5 model and RCP (i.e. all time periods combined) (**Figures 3.5b** and **3.6b**, **Table 3.5**). Furthermore, when range area outcomes were separated only by RCP (i.e. all time periods and

CMIP5 models combined), CMIP5 model (i.e. all time periods and RCPs combined), or time period (i.e. all CMIP5 models and RCPs combined), variability in range area was highest within RCPs (**Figure 3.6a**), high within CMIP5 models (**Figure 3.5a**), and lowest within time periods (**Figure 3.4a**) (**Table 3.5**). These outcomes suggest that the largest variation in range area for all 18 climate futures is introduced primarily by differences between time periods, followed by CMIP5 models, then by RCPs.

Variability was smallest for the CanESM2 model in the 2080s and for RCP 8.5 in the 2080s (note that all outcomes associated with these scenarios predict essentially no remaining range area) (**Figures 3.4a** and **3.4b**, **Table 3.5**). Outcomes were most variable for the 2020s and least variable for the 2080s, regardless of CMIP5 model or RCP (**Figures 3.4a** and **3.4b**, **Table 3.5**). Consistent with this is that for outcomes separated by only time period (i.e. all CMIP5 models and RCPs combined), the 2020s contained the most variation, followed by the 2050s and the 2080s (**Figure 3.4a**, **Table 3.5**). Like with time periods, outcomes were most variable under RCP 4.5 than RCP 8.5, regardless of time period or CMIP5 model (**Figures 3.6a** and **3.6b**, **Table 3.5**). Consistent with this is that for outcomes separated only by RCP (i.e. all time periods and CMIP5 models combined), RCP 4.5 contained more variation than RCP 8.5 (**Figure 3.6a**, **Table 3.5**).

However, unlike with time periods and RCPs, relative variability in CMIP5 models depended on whether time periods or RCPs were combined. When outcomes were grouped by CMIP5 model and time period (i.e. RCPs are combined), CCSM4 contained the most variation, followed by CNRM-CM5 and CanESM2 in each time period (**Figure 3.5a**, **Table 3.5**). When outcomes were grouped by RCP and CMIP5 model (i.e. time periods are combined), CCSM4 contained the most variation, followed by CanESM2 and CNRM-CM5 under each RCP (**Figure 3.5b**, **Table 3.5**).

The overall effect is that when outcomes were separated only by CMIP5 model (i.e. all time periods and RCPs combined), CanESM2 contained more variability than CNRM-CM5 (**Figure 3.5a**, **Table 3.5**).

All time periods had higher and more similar levels of variability under CCSM4 (**Figure 3.4a**, **Table 3.5**). Although variability remained high for the 2020s under CNRM-CM5 and CanESM2, it was lower for the other two time periods under these CMIP5 models (**Figure 3.4a**, **Table 3.5**). Likewise, all CMIP5 models had higher and more similar levels of variability in the 2020s (**Figure 3.5a**, **Table 3.5**). Although variability remained high for CCSM4 in the 2050s and 2080s, it was lower for the other two CMIP5 models in these time periods (**Figure 3.5a**, **Table 3.5**).

Similarly, all time periods had higher and more similar levels of variability under RCP 4.5, with noticeably lower variability only in later time periods under RCP 8.5 (**Figure 3.4b**, **Table 3.5**). Likewise, both RCPs had higher and more similar levels of variability in the 2020s, with noticeably lower variability in later time periods only under RCP 8.5 (**Figure 3.6a**, **Table 3.5**).

Finally, all CMIP5 models had higher and more similar levels of variability under RCP 4.5, with somewhat lower variability only under RCP 8.5 in the other two climate models (**Figure 3.5b**, **Table 3.5**). Likewise, both RCPs had higher and more similar levels of variability under CCSM4, with somewhat lower variability in the other two climate models only under RCP 8.5 (**Figure 3.6b**, **Table 3.5**).

Table 3.2. Average percentage reductions in *Lynx canadensis* habitat metrics across time periods and climate scenarios within the study area.

	CMIP 5 Model	RCP	2020s	2050s	2080s
Core Numbers	CCSM4	4.5	23%	62%	62%
	CCSM4	8.5	38%	69%	100%
	CNRM-CM5	4.5	46%	69%	92%
	CNRM-CM5	8.5	54%	77%	100%
	CanESM2	4.5	46%	77%	100%
	CanESM2	8.5	38%	100%	100%
	All	**All**	41%	76%	92%
Range Area (km^2)	CCSM4	4.5	27%	77%	88%
	CCSM4	8.5	45%	93%	100%
	CNRM-CM5	4.5	47%	90%	98%
	CNRM-CM5	8.5	65%	95%	100%
	CanESM2	4.5	47%	94%	100%
	CanESM2	8.5	61%	100%	100%
	All	**All**	49%	92%	98%
Total Core Area (km^2)	CCSM4	4.5	29%	82%	91%
	CCSM4	8.5	49%	96%	100%
	CNRM-CM5	4.5	48%	92%	99%
	CNRM-CM5	8.5	68%	96%	100%
	CanESM2	4.5	51%	96%	100%
	CanESM2	8.5	65%	100%	100%
	All	**All**	51%	94%	98%
Average Per Core Area (km^2)	CCSM4	4.5	7%	53%	77%
	CCSM4	8.5	17%	86%	NA
	CNRM-CM5	4.5	3%	74%	87%
	CNRM-CM5	8.5	30%	85%	NA
	CanESM2	4.5	8%	85%	NA
	CanESM2	8.5	44%	NA	NA
	All	**All**	18%	74%	79%
Average Core Suitability (0.38 – 1)	CCSM4	4.5	0%	12%	13%
	CCSM4	8.5	2%	14%	NA
	CNRM-CM5	4.5	5%	14%	24%
	CNRM-CM5	8.5	6%	16%	NA
	CanESM2	4.5	0%	13%	NA
	CanESM2	8.5	10%	NA	NA
	All	**All**	4%	14%	15%

NA = not applicable (no cores predicted). RCP = Representative Concentration Pathway. CMIP5 = Coupled Model Intercomparison Project Phase 5.

Table 3.3. Habitat metrics across time periods and climate scenarios for *Lynx canadensis* habitats within the study area.

	CMIP 5 Model	RCP	Present	2020s	2050s	2080s
Core Numbers	Present	NA	13	-	-	-
	CCSM4	4.5	-	10	5	5
	CCSM4	8.5	-	8	4	0
	CNRM-CM5	4.5	-	7	4	1
	CNRM-CM5	8.5	-	6	3	0
	CanESM2	4.5	-	7	3	0
	CanESM2	8.5	-	8	0	0
	All	**All**	-	7.67	3.17	1.00
Range Area (km^2)	Present	NA	28492	-	-	-
	CCSM4	4.5	-	20747	6599	3517
	CCSM4	8.5	-	15702	1906	0
	CNRM-CM5	4.5	-	15069	2780	560
	CNRM-CM5	8.5	-	9871	1365	0
	CanESM2	4.5	-	15124	1596	43
	CanESM2	8.5	-	10978	25	2
	All	**All**	-			

Table 3.3 is continued on page 114.

NA = not applicable (no cores predicted). RCP = Representative Concentration Pathway. CMIP5 = Coupled Model Intercomparison Project Phase 5.

Table 3.3. (cont'd) Habitat metrics across time periods and climate scenarios for *Lynx canadensis* habitats within the study area.

	CMIP 5 Model	RCP	Present	2020s	2050s	2080s
Total Core Area (km^2)	Present	NA	26340	-	-	-
	CCSM4	4.5	-	18811	4780	2312
	CCSM4	8.5	-	13465	1154	0
	CNRM-CM5	4.5	-	13730	2105	273
	CNRM-CM5	8.5	-	8524	941	0
	CanESM2	4.5	-	13029	924	0
	CanESM2	8.5	-	9129	0	0
	All	**All**	-	12781.33	1650.67	430.83
Average Per Core Area (km^2)	Present	NA	2026	-	-	-
	CCSM4	4.5	-	1881	956	462
	CCSM4	8.5	-	1683	289	NA
	CNRM-CM5	4.5	-	1961	526	273
	CNRM-CM5	8.5	-	1421	314	NA
	CanESM2	4.5	-	1861	308	NA
	CanESM2	8.5	-	1141	NA	NA
	All	**All**	-	1667.13	521.26	430.83
Average Core Suitability (0.38 – 1)	Present	NA	0.58	-	-	-
	CCSM4	4.5	-	0.58	0.51	0.50
	CCSM4	8.5	-	0.57	0.50	NA
	CNRM-CM5	4.5	-	0.55	0.50	0.44
	CNRM-CM5	8.5	-	0.54	0.49	NA
	CanESM2	4.5	-	0.58	0.50	NA
	CanESM2	8.5	-	0.52	NA	NA
	All	**All**	-	0.56	0.50	0.49

NA = not applicable (no cores predicted). RCP = Representative Concentration Pathway. CMIP5 = Coupled Model Intercomparison Project Phase 5.

Table 3.4. Average percentage reductions in *Lynx canadensis* habitat metrics within the study area aggregated by climate scenario and ranked by impact

	Rank	CMIP 5 Model	RCP	Core No.	Range Area (km^2)	Total Core Area (km^2)
By CMIP5 Model and RCP	1	CCSM4	4.5	49%	64%	67%
	2	CNRM-CM5	4.5	69%	78%	80%
	3	CCSM4	8.5	69%	79%	81%
	4	CanESM2	4.5	74%	80%	82%
	5	CNRM-CM5	8.5	77%	87%	88%
	6	CanESM2	8.5	79%	87%	88%
By CMIP5 Model	1	CCSM4	All	59%	72%	74%
	2	CNRM-CM5	All	73%	83%	84%
	3	CanESM2	All	77%	84%	85%
By RCP	1	All	4.5	64%	74%	76%
	2	All	8.5	75%	84%	86%

RCP = Representative Concentration Pathway. CMIP5 = Coupled Model Intercomparison Project Phase 5. Scenarios are ranked by impact on habitat suitability, where low numbers indicate lowest impact.

Table 3.5. Variability in total range area for *Lynx canadensis* within the study area aggregated across time periods and climate scenarios.

	Time	RCP	CMIP5 Model	Mean Area (km^2)	n	SD	Min	Max
By Time Period	Present	-	-	28492	1	-	-	-
	2025	All	All	14582	6	3534.94	9871	20747
	2055	All	All	2379	6	2056.52	25	6599
	2085	All	All	687	6	1281.47	0	3517
By RCP	Future	4.5	All	7337	9	7212.97	43	20747
	Future	8.5	All	4428	9	5711.24	0	15702
By CMIP5 Model	Future	All	CCSM4	8079	6	7582.51	0	20747
	Future	All	CNRM-CM5	4941	6	5596.81	0	15069
	Future	All	CanESM2	4628	6	6100.43	2	15124
By Time Period and RCP	2025	4.5	All	16980	3	2663.77	15069	20747
	2055	4.5	All	3658	3	2134.81	1596	6599
	2085	4.5	All	1373	3	1530.43	43	3517
	2025	8.5	All	12184	3	2528.55	9871	15702
	2055	8.5	All	1099	3	790.67	25	1906
	2085	8.5	All	1	3	0.94	0	2
By Time Period and CMIP5 Model	2025	All	CanESM2	13051	2	2073.00	10978	15124
	2055	All	CanESM2	811	2	785.50	25	1596
	2085	All	CanESM2	23	2	20.50	2	43
	2025	All	CCSM4	18225	2	2522.50	15702	20747
	2055	All	CCSM4	4253	2	2346.50	1906	6599
	2085	All	CCSM4	1759	2	1758.50	0	3517
	2025	All	CNRM-CM5	12470	2	2599.00	9871	15069
	2055	All	CNRM-CM5	2073	2	707.50	1365	2780
	2085	All	CNRM-CM5	280	2	280.00	0	560
By CMIP5 Model and RCP	Future	4.5	CCSM4	10288	3	7502.13	3517	20747
	Future	4.5	CNRM-CM5	6136	3	6381.04	560	15069
	Future	4.5	CanESM2	5588	3	6772.95	43	15124
	Future	8.5	CCSM4	5869	3	6996.15	0	15702
	Future	8.5	CNRM-CM5	3745	3	4367.20	0	9871
	Future	8.5	CanESM2	3668	3	5168.72	2	10978

RCP = Representative Concentration Pathway. CMIP5 = Coupled Model Intercomparison Project Phase 5.

Habitat Suitability and Core-Habitat Projections

For present day projections, the largest habitat cores with the highest suitability were centralized within the northern portion of the study area (**Figure 3.7**), with residual smaller, lower suitability cores distributed throughout the central and southeastern portion of the study area. A moderately sized core was projected farther west within the Thompson-Okanagan Plateau, and the largest core was a well-connected core beginning at the northernmost end of the study area over the eastern side of the Interior Transition Ranges and the core of the Thompson-Okanagan Plateau, extending southward into the Okanogan Range and the North Cascades. This core overlapped the Okanogan LMZ and lynx critical habitat in Washington State, covering roughly 25% of the LMZ and roughly 35% of critical habitat. Also within the LMZ, and within overlapping critical habitat, two additional smaller unconnected cores were projected, one of higher suitability directly to the south and one of marginal suitability within the northeastern portion partially coinciding with the Loomis State Forest, for a total of core area of 2,501 km^2 within the Okanogan LMZ. Three small marginal to high suitability cores at the southern end of the North Cascades and within the Eastern Cascades were projected, with an additional three small, marginal to moderate suitability cores in the Blue Mountains of Oregon and one in the Idaho Batholith.

The large core running through the southern end of BC into Washington State was projected to become fragmented into a minimum of four separate cores by the 2020s under all climate scenarios (**Figures 3.8** and **3.9**, **Figures C.2 - C.7**). Fragmentation appeared to increase along a latitudinal gradient from north to south. At this time step, most of the already small cores in the southern part of the study area, the Blue Mountains and the Eastern Cascades, were lost, with the exception of those at the southern end of the North Cascades under the three most conservative scenarios in **Table 3.4**. Under all scenarios but one, CNRM-CM5 RCP 8.5, cores persisted within the Okanogan LMZ and within critical habitat in the 2020s, although decreases in size and especially in suitability were evident in all scenarios. Average core area within the Okanogan LMZ under all scenarios where cores persisted was predicted to be 1,245 km^2 (i.e. a 50% reduction), with a maximum core area of 1,777 km^2 (i.e. a 29% reduction) under the most conservative scenario (CCSM4 RCP 4.5) and a minimum core area of 458 km^2 (i.e. a 82% reduction) under the least conservative scenario (CanESM2 RCP 8.5). Cores were lost entirely in the eastern part of the Okanogan LMZ in the 2020s under CanESM2 RCP 8.5. Between all scenarios for the entire study area, an average of 7.7 cores with an average per core area of 1,167 km^2 and an average suitability of 0.56 was predicted.

Fragmentation of cores progressed in the 2050s, with all previously larger cores becoming smaller, poorer, and losing continuity in all scenarios, especially along the southern margin (**Figures 3.8** and **3.9**, **Figures C.8 - C.13**). Fragmentation was severe under all scenarios, with the majority of core area within the study area lost by this point. Core habitats within the Okanogan LMZ and within critical habitat vanished under all scenarios for this time period. CCSM4 RCP 4.5 appeared least severe, with five small to medium sized cores of marginal to high suitability remaining in the northern portion of the study area. Effects were most severe under the CanESM2 RCP 8.5 scenarios, under which all core areas are lost from the study area in the 2050s. Across the study area, projections predicted an average for all scenarios of 3.2 cores, 521 km^2 of per core area, and 0.50 per core suitability (**Table 3.2**).

Impacts in the 2080s were most extreme (**Figures 3.8** and **3.9**, **Figures C.14 - C.19**). All scenarios but two, CCSM4 RCP 4.5 and CNRM-CM5 RCP 4.5, predicted all core areas would disappear from the study area. CCSM4 RCP 4.5 was the most optimistic scenario, predicting five cores remaining in the most northerly portion of the study area with an average per core area of 462 km^2 and an average suitability of 0.50, roughly equivalent to the average outcome for the 2050s under all combined scenarios.

Core shrinkage over all time periods reveal areas where cores are more likely to persist under the best case scenario (**Figure 3.10**). Within the Okanogan LMZ in the 2020s, the largest most suitable core areas in all scenarios extended down from the Washington-BC border into the western portion of the Okanogan National Forest, and to a lesser extent, across into the eastern portion and the northwestern part of the Loomis State Forest. The most conservative scenario, CCSM4 RCP 4.5, predicted that some core area will remain in the Black Pine Basin.

Several additional cores to the north, though shrinking or expanding between time periods and climate scenarios, shared common centers through time periods (**Figure 3.10**). The most southerly core in BC was predicted to be centered within the Okanogan Range, and in the 2020s, it was predicted to overlap the eastern portion of Manning Provincial Park and Cathedral Provincial Park to the east, and extend north to just short of Highway 3 on the east and to just short of the Tulameen River on the west. An additional larger, higher-suitability core was predicted within the central to southern portion of the Thompson-Okanagan Plateau, with a series of higher suitability cores just to the north between the Clear Range and the Douglas Plateau. The most easterly predicted core was centered over the Okanagan Highlands, running south and east of Myra-Bellevue Provincial Park.

Environmental Novelty

Environmental novelty depicted in MESS outputs (**Figures 3.11** and **3.12**) was similar in geographic distribution to environmental novelty for present-day habitat projections (**Figure**

2.15), with environmental similarity generally projected through parts of the North Cascades, the Okanogan Highlands, the Blue Mountains, and the Cascades to the south. Environmental novelty was low in areas where cores were projected, but higher in the northeast, south-central, and coastal portions of the study area. Novelty increased in magnitude and extent in these areas through time and under more extreme climate scenarios. For example, the highest environmental novelty was predicted for the CanESM2 RCP 8.5 scenario in the 2080s. Environmental novelty was lowest under the CCSM4 model, intermediate under the CNRM-CM5 model, and highest under the CanESM2 model. When compared between RCP 4.5 and 8.5, it was higher under RCP 8.5.

Discussion

These projections represent a substantial contribution to understanding of potential futures for lynx in the Washington-BC transboundary region, calling attention to the need to evaluate region-specific outcomes based on unique regional habitat-selection drivers. They also offer smaller-scale, finer-resolution delineation of potential outcomes for the Washington-BC transboundary region along with an exploration of uncertainty in climate futures that managers can use to contextualize likely changes. Outcomes inform consideration of what will be the most effective management for southern periphery lynx in this area going forward. Here, I frame likely outcomes and variability of outcomes in a broader context, discuss whether results are consistent with expectations, and explore implications for lynx in Washington State. I also compare results with previous local-scale, broad-scale, and regional studies. I conclude by discussing the caveats and assumptions that managers should consider when applying these results, providing recommendations for future research and outlining conservation applications and implications.

Outlooks for Washington-BC Canada Lynx

Projections for present-day suitable cores aligned well with the Okanogan LMZ and lynx critical habitat in Washington State, overlapping the western portion of the Okanogan National Forest, the Black Pine Basin, and the Loomis State Forest. Within the Okanogan LMZ, no cores were projected to exist south of Lake Chelan, where lynx populations have not been observed since 1991 (Vanbianchi 2015). As expected, the most contiguous and highly suitable cores were projected within the northern portion of the study area, with the largest core extending from near the northern boundary of the study area in BC into Washington State. Contrary to expectations, multiple small, marginally suitable cores were projected south of the Okanogan LMZ, with several in Oregon and even Idaho.

Climate outlooks for lynx within the study under future climate scenarios are poor. As expected, fragmentation and loss of lynx habitat cores within the study area increased through time in all scenarios, with reductions in number of cores, total and per core area, and average core suitability through time. Also consistent with expectations, though evident throughout the study area, fragmentation and loss of habitat were visibly higher in the south, the hallmark of a northward range shift. Fragmentation was severe under all scenarios and all time periods, especially in the 2050s and 2080s, but impacts in the 2020s were not negligible, with an average reduction across scenarios in total core area within the study area of 51%. However, it is probable that core habitats will continue to exist through the 2020s both within the study area and the Okanogan LMZ, with only one scenario in disagreement (i.e. CNRM-CM5 RCP 8.5).

The outlook changed drastically in the 2050s, with an average reduction across scenarios in total core area within the study area of 94%. All outcomes suggest that by this time period, lynx habitat cores within the Okanogan LMZ will disappear. However, it is probable that habitat cores will continue to exist in the northern portion of the study area, with only one scenario in disagreement (i.e. CanESM2 RCP 8.5). By the 2080s, outcomes lean toward no core habitat within the study area, with an average reduction across scenarios in total core area of 98%. Only two scenarios, CCSM4 RCP 4.5 and CNRM-CM5 RCP 4.5, suggest that small, marginally suitable core areas may remain in the northern portion of the study area. Patchy and likely subpar suitability, similar to present day suitability over the southern half of the study area, persisted under some other more conservative scenarios in the north-central portion of the study area.

Comparison of Outcomes with Previous Studies

Estimates of total core area within Washington State and within the Okanogan LMZ are similar to previous estimates by Koehler et al. (2008) but lower than those by Vanbianchi (2015). Differences exist in areas projected to be suitable between my analysis and previous studies, with my study contradicting past regional habitat estimates for the present day that showed suitability south of Lake Chelan and in the Okanogan Highlands. Koehler et al. (2008) estimated a total of 3,800 km^2 of suitable habitat in Washington State compared to my estimate 3,642 km^2. However, it should be noted that Koehler et al. (2008) used thresholds from a regression model to map suitable winter habitat and that substantial differences in the placement of suitable habitat exist, with no cores projected by my core-habitat model in the Okanogan Highlands, including areas within the Vulcan-Tunk, Kettle Range, the Wedge, Little Pend Oreille, and Salmo Priest LMZs. However, my estimate for total core area within the Okanogan LMZ at 2,501 km^2 is also very close to the Koehler et al. (2008) estimate for Chelan and western Okanogan counties at 2,411 km^2. Vanbianchi (2015) estimated roughly 4,600 km^2 of total core area within the Okanogan LMZ, which is noticeably higher. This difference is largely explained by differences in projected core areas between the studies, as Vanbianchi (2015) projected several suitable cores south of Lake Chelan within the LMZ, an area with no projected suitable cores in my model. Without these cores, the estimate is reduced to roughly 3,400 km^2, approximately 35% higher than mine.

Comparisons of outcomes under climate futures are made difficult by the different GCMs and emission pathways used in previous studies. In general, my results support previous broad-scale and regional studies that predict northward shifts and reduced range size for lynx throughout the southern periphery (Carroll 2007, Gonzalez et al. 2007, Peers et al. 2014). However, within the Washington-BC transboundary region, results indicate much more extreme range retraction and fragmentation than within the southern periphery of lynx range in general (Gonzalez et al. 2007, Peers et al. 2014) and when compared to other regions (Carroll 2007).

Using an ensemble of three GCMs under the A1B scenario, intermediate between RCP 4.5 and 8.5, Gonzalez et al. (2007) predicted a 200-km northward shift by 2100, somewhat less than the distance between the southern edge of presently suitable habitats in the Okanogan LMZ and the northern boundary of my study area (~250 km), also likely to be unsuitable by the 2080s. My result of no habitat within the U.S. portion of the study area by 2055 is also more extreme than the two-thirds loss across the entire U.S. projected by Gonzalez et al. (2007) by 2100. Similarly, my estimates are more extreme than those of the Peers et al. (2014) study. Peers et al. (2014) projected a 29.14% loss for the 2050s and a 50.98% loss for the 2080s within all North American southern periphery habitat under the A2 scenario. The most closely corresponding values of range reduction from my projections were 96% and 100% respectively. Finally, Carroll (2007) found lynx populations at their range margin were reduced by 59% within a transboundary study area in eastern North America under the SRES A2 2055 scenario. The SRES A2 scenario is most similar to the RCP 8.5 scenario in my analysis (Glick et al. 2011). If habitat area is assumed to be directly proportional to population size, a rather substantial assumption, average predicted reduction under RCP 8.5 (97%) suggest a much more extreme outcome for the Washington-BC study area.

I attribute differences primarily to variation in continuity and area of suitable habitats throughout the much larger areas assessed in these broader-scale studies. Compared to some areas within the southern periphery of the lynx range as demarcated by Peers et al. (2014) and Gonzalez et al. (2007), projected suitable range in the region corresponding to my study area was substantially more fragmented and dispersed. Lynx habitat in Washington State is known to be generally smaller and more fragmented than other lynx habitats throughout the U.S. This is a point substantiated by these broad-scale studies as well. Gonzalez et al. (2007) predicted a very small area of suitable habitat within Washington State for the present day, and for this reason, considered it to be highly vulnerable. Compared to some areas within the southern periphery as demarcated by Peers et al. (2014), projected suitable range in the region corresponding to my study area was substantially more fragmented and dispersed. Average reductions computed over broad areas are likely to mask regional variation.

It should also be noted that my projections estimate large differences in distribution and amount of suitable habitat compared to broad-scale studies. Present suitability in the Gonzalez et al. (2007) study is reduced substantially in the North Cascades as well as in areas of BC currently thought to be the source of immigration into Washington State. In the Peers et al. (2014) study, suitable habitat is projected to extend across a wider longitudinal band beginning in the North Cascades and ending in the northern half of Oregon.

Uncertainty in Climate Futures

Consistent with expectations, the most favorable outlook for lynx was found for the scenario with the smallest temperature increase across all time periods, CCSM4 RCP 4.5, whereas the least favorable was, generally, found for the scenario with the highest temperature increase across all time periods, CanESM2 RCP 8.5. The only exceptions are CNRM-CM5 RCP 8.5 and RCP 4.5 in the 2020s, with stronger impacts in the Washington State portion of the study area than CanESM2 scenarios under the same RCPs. In terms of primary metrics (i.e. total core area, number of cores, and range size), outcomes under all other scenarios were intermediate between the two other climate models, but when considered for all time periods, these outcomes are closer to outcomes under CanESM2.

As expected, outcomes varied widely between climate scenarios and time periods for the study area, with core area reduced 29 – 68% in the 2020s, 82 – 100% in the 2050s, and 91 – 100% in the 2080s. Also as expected, variability was reduced most when outcomes for different time periods were considered separately. However, contrary to expectations, differences between CMIP5 models contributed somewhat more to variability of range area in each time period than did differences in RCPs, suggesting that the specific GCM model configuration and resulting internal variation are important in this case (Glick et al. 2011). Range area outcomes under more extreme scenarios (i.e. later time periods, CMIP5 models with larger temperature anomalies, and RCP 8.5) contained far less variability than those under less extreme scenarios. Levels of variability were higher and more similar to each other for less extreme scenarios. This result is intuitive when it is considered that more drastic changes are likely to reduce range area toward zero, thereby leaving less room for variation. Despite this, results still indicate that unfavorable outcomes under more extreme scenarios are more certain.

Not surprisingly, when outcomes were grouped by CMIP5 model alone, CNRM-CM5 (i.e. lower temperature anomaly) contained more variability than CanESM2 (i.e. higher temperature anomaly) This switch is due to CNRM-CM5 and CanESM2 trading places as the most extreme climate scenario in the 2020s, where unlike in other time periods, CanESM2 outcomes were more favorable than CNRM-CM5 outcomes.

Although boxplots indicated that uncertainty in impacts may be much lower for later time periods and more extreme climate scenarios, MESS maps indicated that confidence in the models from which metrics of suitability were derived for earlier time periods and less extreme climate scenarios was somewhat higher. However, across time periods and climate scenarios, environmental novelty was generally low within the areas where cores were predicted and within the areas where climates are likely to be favorable toward the existence of cores. For example, the south-central and coastal portions of the study area, with somewhat high environmental novelty under climate futures, are presently not suitable for lynx and are not likely become suitable. One exception is the northeast corner of the study area, a region wherein some areas are currently thought to be suitable for lynx and where my models did not predict suitability, even for the present-day.

Caveats and Assumptions

Models used to project habitat suitability for the present day and under future climates have many limitations. As model configuration for the core-habitat suitability model impacts projections under climate change, the caveats discussed in *Chapter 2* also apply, including the clustered nature of the training samples and lack of an independent test dataset with which to examine model performance in areas farther from the training samples. The projected absence of suitable cores in certain areas where suitability historically occurred but is now questionable, including areas south of Lake Chelan within the Okanogan LMZ and areas in the Okanogan Highlands such as the Kettle Range, is notable. As in *Chapter 2*, I attribute this primarily to limitations presented by the clustered nature of the training samples, where it is unknown if lynx in more distant areas select habitat in a manner that is fundamentally different. It is also possible that these areas are no longer suitable. Nevertheless, model results should be interpreted and applied with caution, especially projections for areas most removed from training samples. Sensitivity to core mapping techniques was not evaluated. As such, cores are representative of conceptual patches more than actual patches of habitat suitability. Actual extent, size, and suitability is likely to vary, though perhaps less than location.

The scope of the methods limited models to consideration of present-day habitat relationships at a regional extent and at a resolution of 1 km. **Table 3.6** provides a list of some of the factors that these models do not account for, grouped by functional category. Distinctions between habitat selection and habitat suitability, including competition dynamics not mediated by differences in snow conditions, mortality risks, and intersexual and seasonal differences, are discussed in *Chapter 2*. For each of the other limitations, examples and implications for outcomes are discussed here.

Adaptive Responses

Future changes in relationships with environmental predictors may influence outcomes in ways not accounted for in these projections. If in response to environmental stress, lynx are able to change the extent to which they rely on certain environmental factors, outcomes may improve. For example, the potential for prey switching away from lynx reliance on snowshoe hares (*Lepus americanus*) has been explored in some studies. However, although lynx are known to forage opportunistically on red squirrels (*Tamiasciurus hudsonicus*) and other alternative prey, such as Columbian ground squirrels (*Urocitellus columbianus*), when and where available (Aubry et al. 2000, Roth et al. 2007, Squires and Ruggiero 2007), the general consensus is that high snowshoe hare densities are needed to sustain lynx (Ward and Krebs 1985, Mowat et al. 2000, Ruggiero et al. 2000, Schwartz et al. 2002). Changes in genetic or functional resilience are another consideration. Reductions in genetic diversity due to habitat fragmentation and geographic barriers imposed under climate change may reduce adaptive capacity for lynx (Koen et al. 2014). This may reduce tolerance to certain environmental conditions, essentially effecting a shift in habitat-selection drivers, which would reduce suitability.

Environmental Novelty and Altered Biotic Interactions

Models did not account for changes in human land use in future time periods, such as new highway construction projects, shifts in the placement of housing centers, urban expansion, and changes to recreation within wilderness areas. Such changes will impact the outcomes projected by these models to the extent that lynx are reliant on these factors. Although MESS maps indicated overall low levels of environmental novelty for included predictors where suitable habitats are projected to occur, introduction of novel environmental conditions outside those present in model training can introduce further uncertainty to these outcomes.

Another factor that comes into play when projecting habitat into the future is that lynx are commonly associated with Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine (*Pinus contorta*) vegetation types. Although these models did not include vegetation type as a predictor, climatic factors that define the bioclimatic niche of these important vegetation types were included. Lags in vegetation shift are likely to occur under future conditions. To the degree to which these lags occur and to the degree to which habitat selection in these models was indirectly tied to vegetation, fragmentation and range reduction may be reduced in some cases.

Finally, changes in the biotic interactions that drive selection can either ameliorate or exacerbate outcomes. Relationships under climate change may not persist (i.e. may not be static). For example, returning to the question of the model’s treatment of competition dynamics discussed in *Chapter 2*, recall that to the extent that the model includes interactions between lynx and their competitors that are driven by the surrogates for snow conditions included in the model, predictions incorporate some competition dynamics. However, just as competition dynamics presently mediated by factors outside the model can change outcomes, so can any changes to drivers of competitive interactions, including those drivers codified in the model.

Extreme Events

Models did not include predictors that are likely to represent stochastic or extreme disturbances. Wildfires are an example of localized, stochastic disturbances that can greatly influence habitat suitability. An important example is the 2006 Tripod fire that burned most of the Koehler et al. (2008) Meadows study area. Predictors descriptive of selection with respect to burned areas were absent from the models due to the temporal and geographic scale of the models being coarser than that at which these drivers operate. As such, models for the present day predicted high levels of suitability within the perimeter of the Tripod fire. Extreme events of a stochastic nature are perhaps among the largest contributors to why these models provide only potential suitability. Stochastic events combined with poor suitability or borderline insufficient core sizes could put affected lynx populations at serious risk.

Furthermore, although models balanced training data across seasons, they used annual, albeit seasonally biased, climatic variables as predictors and did not differentiate between habitat-selection drivers in different seasons. As such, seasonal variance is not fully accounted for and outcomes reflect mean potential outcomes. Impacts from seasonal extremes may have the capacity to dominate suitability under certain circumstances. For example, an unusually warm or dry winter could open up otherwise suitable habitats to encroaching bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) (Interagency Lynx Biology Team 2013), temporarily displacing lynx.

Overall Implications of Limitations

Model outcomes represent potential habitat suitability and should be interpreted with caution and with these limitations in mind. Furthermore, suitability is not a direct indicator of population resilience. Factors such as continued access to suitable habitats, demographic stochasticity, and the Allee effect are strong influences on population persistence at range margins (Anderson et al. 2009), even where suitability is high.

Table 3.6. Factors to be considered in interpretation of *Lynx canadensis* habitat suitability and core-habitat projections for the Washington-British Columbia transboundary region.

Functional Group	**Description***
Habitat Selection vs. Suitability (*Chapter 2*)	Interference and exploitation competition dynamics mediated by predictors not included in the model Unperceived mortality risk Intersexual and seasonal differences in selection
Adaptive Response (*Chapter 3*)	Future changes in relationships with environmental predictors
Environmental Novelty and Altered Biotic Interactions (*Chapter 3*)	Changes in human land use under future climates Environmental conditions not present at the time of model calibration Changes to relationships that drive interactions with interference and exploitation competitors Lags in vegetation composition changes
Extreme Events (*Chapter 3*)	Stochastic disturbances that alter habitat at local scales Seasonal extremes in climate

* Limitations apply to outcomes to the extent that lynx habitat suitability is defined by each of the factors described.

Recommendations for Future Research

I recommend that future research evaluate the factors outlined above as these factors could change the outcomes substantially. Several of these recommendations are discussed in *Chapter 2*, including evaluating for differences in habitat selection between regions farther from the Loomis State Forest and Black Pine Basin and identifying intersexual and seasonal differences in habitat suitability.

In the case of exploring projected suitability under climate change, adaptive potential is an area in need of further research. Research in this area will help determine whether relationships with habitat are static and thus whether in situ persistence is possible. However, without exposure to change it may be difficult to ascertain whether lynx are adapting. Likely most pertinent to this question is whether lynx reliance on snowshoe hares will continue and to what extent. Although some research suggests that lynx are capable of some opportunistic foraging when exposed to environmental stress, the degree to which this will increase, if at all, under a changing climate is not known. Previous research on hare densities needed to support lynx and current presence of lynx only in areas with sufficient hare densities (Ward and Krebs 1985, Mowat et al. 2000, Ruggiero et al. 2000, Schwartz et al. 2002, Roth et al. 2007) suggests that substantial increases in permanent prey switching where hare densities are low are not likely.

In the future, as present lynx habitats become less dominated by prolonged, deep snow, competitive interactions with bobcats and coyotes are likely to increase (Interagency Lynx Biology Team 2013). Understanding of how lynx habitats are likely to shift would benefit from studies that explore factors that mediate competition dynamics, including snow conditions, diet overlap, dispersal ability, dispersal habitat selection, and other habitat requirements. Research should aim to identify specific thresholds in these relationships that will inform management objectives not only with respect to interactions within critical lynx habitat but also with respect to surrounding landscapes where connectivity may be an issue.

Future modeling efforts should seek to separate the importance of vegetation composition from other influences also tied to climate, such as snow cover for lynx. This would allow the import of potential lags in vegetation composition to be fully contextualized. Drivers underlying important predictors in my core-habitat model could not be fully disentangled. In other words, the degree of importance for each predictor owing to its effect on the vegetation could not be determined.

As habitat suitability by itself is not a measure of population persistence, research on the importance of connectivity, particularly under a future showing increases in habitat fragmentation, should be pursued. Connectivity research is important for two reasons: (1) Washington State populations may suffer as connectivity drops with BC, a source of substantial immigration into Washington State, as distances between core habitats begin to exceed the average lynx dispersal distance of roughly 100 km, and (2) if range shifts are unavoidable, reincorporation of genetic and functional diversity from populations at range margins may enhance resilience of larger populations. Although lynx are generally known for their dispersal plasticity, they have been observed to have preferences, including avoidance of open spaces, and limitations, such as large lakes and high topographic relief (Ward and Krebs 1985, Slough and Mowat 1996, Aubry et al. 2000, Mowat et al. 2000, Koehler et al. 2008, Interagency Lynx Biology Team 2013, Squires et al. 2013). One present knowledge gap is whether small, intermediate patches of suitable habitat (i.e. stepping stones) are needed by lynx to reach the phenomenal though rare dispersal distances that have been observed in the past, and if so, what constitutes a stepping stone for lynx (Stinson 2001, U.S. Fish and Wildlife Service 2005).

Conservation Applications and Implications

Overall results suggest similarities between other regional and broad-scale impacts studied and add support to the general trends predicted in these studies. However, large differences between broad-scale projections and other regional projections and my results, including the size and location of present-day suitable habitat and the accelerated rates of change projected for the future within the study area, call attention to the need to evaluate region-specific outcomes that are based on unique regional habitat-selection drivers throughout the range of lynx in the contiguous U.S. These projections also offer delineation of possible outcomes at a finer resolution (i.e. 1 km) and are inclusive of more time periods and climate scenarios, enabling developments over time and the range of uncertainty to be more fully contextualized. Local management should have access to the range of possible outcomes relevant at their management scale to enhance discernment of effective strategies. As such, my results advance our understanding of potential futures for lynx in the Washington-BC transboundary region.

As these projections represent potential and not actual suitability, they should not be interpreted to apply at resolutions finer than 1 km. Size and suitability of projected core habitats should be regarded only in a relative sense as core mapping is not an exact science. Managers should be wary of the imports of the caveats addressed here and of exceptions not included in model formulation that may influence actual future suitability and are encouraged to brainstorm additional exceptions that may apply. Furthermore, managers should be aware of local factors not included in models that can change outcomes for lynx, such as population stochasticity and extreme events.

Managers can get the most out of these projections by considering the context under which they were produced and by prioritizing impacts of actual changes in climate on model forcings (i.e.

the predictors that dominate the model, **Table 3.1**). Continual evaluation of climate trends at regional and local scales is advised to determine which of the climate scenarios used here is most consistent with trends in precipitation and temperature. Given the wide range of variability of outcomes, especially in earlier time steps, as the situation evolves, it will be important to track regional climate change and to use these projections to envision whether impacts will be less or more extreme. Although GCMs were specifically selected to incorporate a broad range of temperate and precipitation anomalies, from among 41 CMIP5 GCMs (Rupp et al. 2013), I explored the range of variability for only three. Expectations should be adjusted accordingly if climate trends appear to deviate outside this range. For example, because the most important drivers in this model were mainly temperature-driven effects (**Table 3.1**), temperature increases greater than those projected within the study area for the models included here are likely to strengthen the impacts.

Regions such as the Kettle Range and forests south of Lake Chelan in the Okanogan LMZ, where lynx populations have historically occurred, should be monitored on a regular basis for lynx populations, especially in light of low projected suitability. This is currently required for LMZs in these regions (Stinson 2001). Projections for areas farther from the Loomis State Forest and Black Pine Basin should be treated with higher scrutiny and lower confidence, until it is determined whether lynx in these regions select habitat differently. Efforts currently underway, including any camera trapping, should be continued in these areas for a time period to determine whether sustainable populations are present. As suggested by Koehler et al. (2008), any plans to reintroduce lynx to these areas or bolster any existing populations would be wise to consider feasibility assessments that evaluate the potential for long-term persistence. As a precursor to expected changes, managers should also consider efforts to reduce impacts in areas to the north in BC, where lynx along with the southern margin of their habitat are likely to shift. As is identified as a need for Washington State (Stinson 2001) and periphery lynx habitat in general (Interagency Lynx Biology Team 2013), human impacts that increase mortality risk and reduce reproductive success should be targeted for mitigation.

At present, current management directed toward minimizing human impacts and managing for lynx habitat needs within Washington State LMZs, especially where suitability is projected to be highest within critical habitat, are likely to be of fundamental importance to ensuring lynx are equipped to respond to the challenges ahead. In 2001, the WDFW advised coordination on management agreements and plans to ensure provisions are outlined for how denning, foraging, and connectivity will be maintained over the long term (Stinson 2001). The conservation measures outlined in the Lynx Conservation Assessment and Strategy (LCAS) report identify specific strategies that may be used to meet this objective (Interagency Lynx Biology Team 2013). One example of this is to manage vegetation to produce a mosaic supportive of the desired snowshoe hare densities, which would include dense early-successional coniferous and mixed-coniferous-deciduous stands as well as mature multi-story coniferous stands. Another is using vegetation management to both maintain and improve horizontal cover for hares.

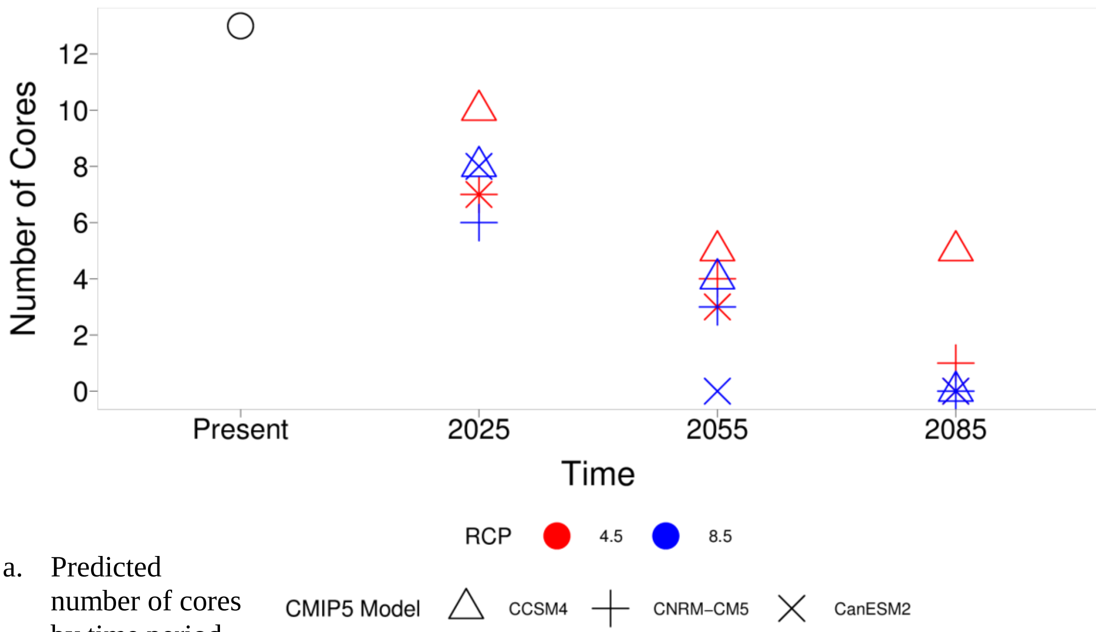
As the situation changes, which my projections suggest will be likely in the near future, efforts should be directed toward monitoring on-the-ground impacts within presently suitable habitat at the southern extent to determine whether lynx are responding as expected, a strategy that has been advised for lynx in this region in general (Stinson 2001) and was included in the objectives of the long-term monitoring plan outlined in the LCAS report. Management objectives should be revised accordingly. Conservation strategies, such as vegetation and wildland fire management and reduction of human-caused habitat fragmentation (Interagency Lynx Biology Team 2013), within those cores most likely to persist under future climates are of primary importance (**Figure 3.10**). However, projections suggest that conservation efforts directed toward cores within the north-central portion of the study area may have value up until roughly 2040, but unless climate trajectories are consistent with the more conservative outlooks discussed, it would be wise to consider whether adaptive responses are possible that mitigate the dire nature of these projections. Without these adaptive responses, efforts to preserve lynx within Washington State may prove ineffective by the 2050s, as would efforts to preserve lynx within the entire study area by the 2080s. If the ability for lynx to adapt in situ is low, it may be wise to consider directing some conservation efforts toward preserving genetic and functional adaptations common in periphery populations.

Managing for connected landscapes is one approach that is designed to promote long-term adaptation, as an alternative or co-requisite to management that seeks solely to promote resistance to change, when this may not be sustainable over the long term (Millar et al. 2007). In their region-specific suggestions, the LCAS advised maintaining connectivity between the North Cascades and Canada. Although projections of core habitats generally suggest that connectivity between BC and the Okanogan LMZ is presently high, connectivity with BC may become an issue as fragmentation progresses. Edge populations are often forced to reckon with environmental stressors not found within the range core, and as such, may adapt genetically and functionally to cope with these stressors (Koen et al. 2014). Contributions to genetic and functional diversity from southern periphery populations may improve the resilience of more northerly populations to climate impacts, whereas complete loss of edge populations may reduce adaptive potential of more centralized populations (Interagency Lynx Biology Team 2013, Koen et al. 2014).

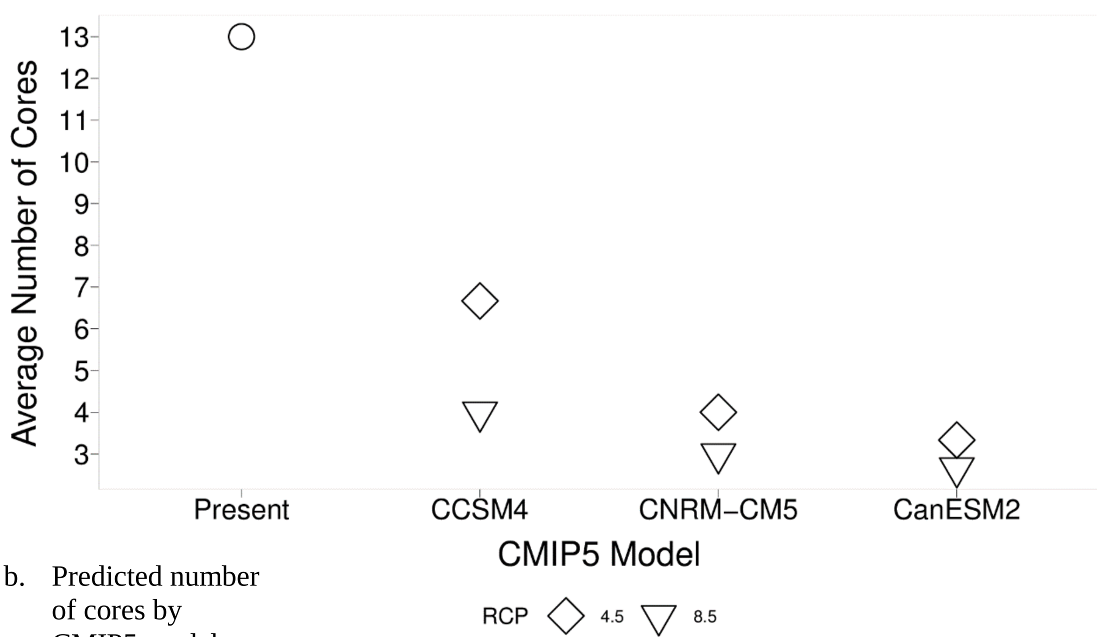
The LCAS describes several approaches that can be used to mitigate habitat fragmentation, including following land use practices that promote or retain conservation of contiguous blocks of lynx habitat and coordination between federal and state agencies with owners of private land adjacent to federal lands to develop conservation easements and explore potential for land exchanges or acquisitions (Interagency Lynx Biology Team 2013). They also suggest that efforts should also be made to mitigate the impact of projects that may jeopardize connectivity at the landscape scale, such as new highway construction projects and expansion of urban centers. Connectivity considerations should be factored in to environmental impact assessments. Where connectivity at the landscape scale is currently reduced by existing human barriers, attempts should be made to identify ways to emulate the level of connectivity that would be present without these features, such as installation of wildlife overpasses (Stinson 2001, Interagency Lynx Biology Team 2013).

Finally, too much connectivity has the potential to facilitate intrusion by lynx competitors and invasive species that may overwhelm survival potential of lynx and other habitat specialists, even as they shift to more suitable climates. Beier et al. (2008) suggest including one or more invasive species in modeling linkages to achieve the appropriate balance between enough and too much connectivity. Managers should remain aware of the implications of increasing connectivity too much in certain ways, and may even consider experimental studies where assisted migration is used as a strategy. One potential option for lynx would be to focus management on maintaining these corridors or stepping stones that facilitate lynx movements but not coyote or bobcat movements.

Figures

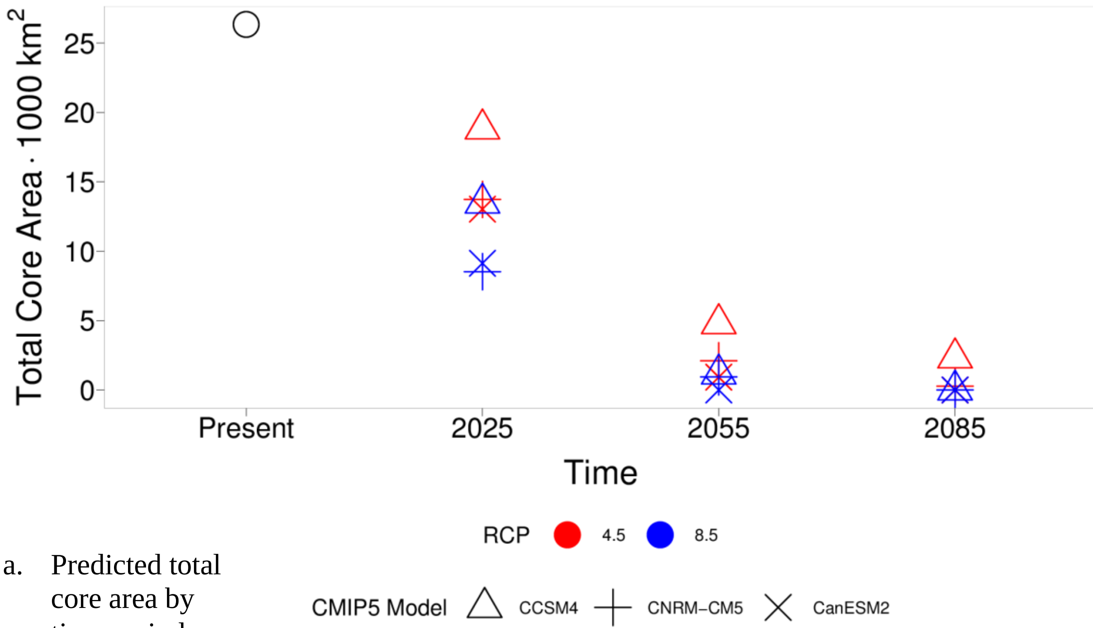


a. Predicted number of cores by time period

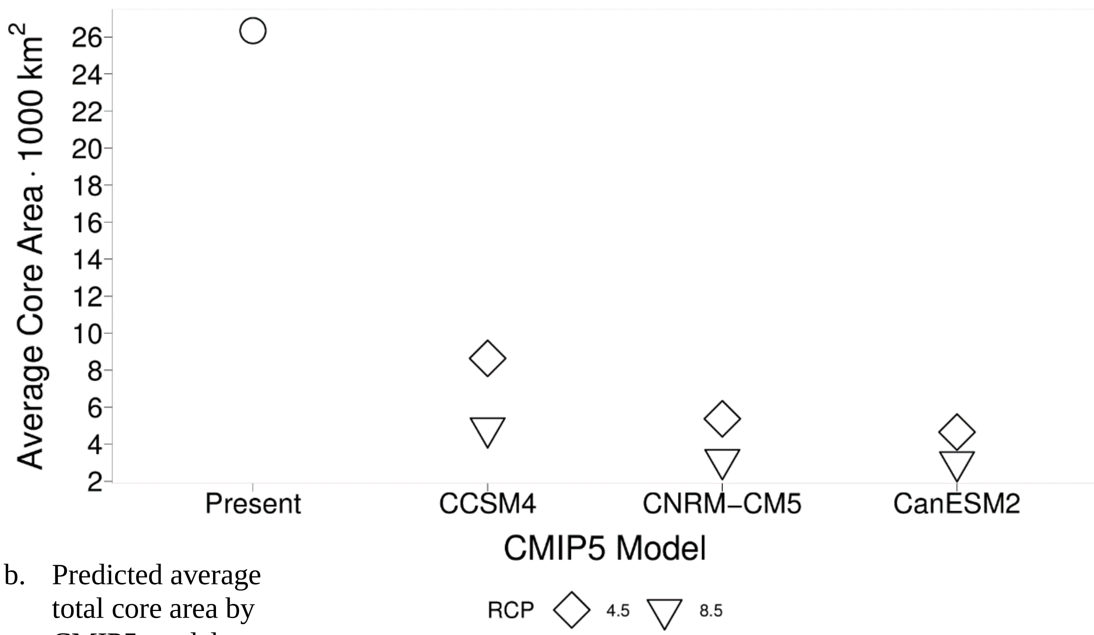


b. Predicted number of cores by CMIP5 model

Figure 3.1. Predicted number of suitable *Lynx canadensis* habitat cores by time period and climate scenario. Plots depict (a) the actual number of cores for each time period, Coupled Model Intercomparison Project Phase 5 (CMIP5) model, and Representative Concentration Pathway (RCP), and (b) the average number of cores by CMIP5 model and RCP.

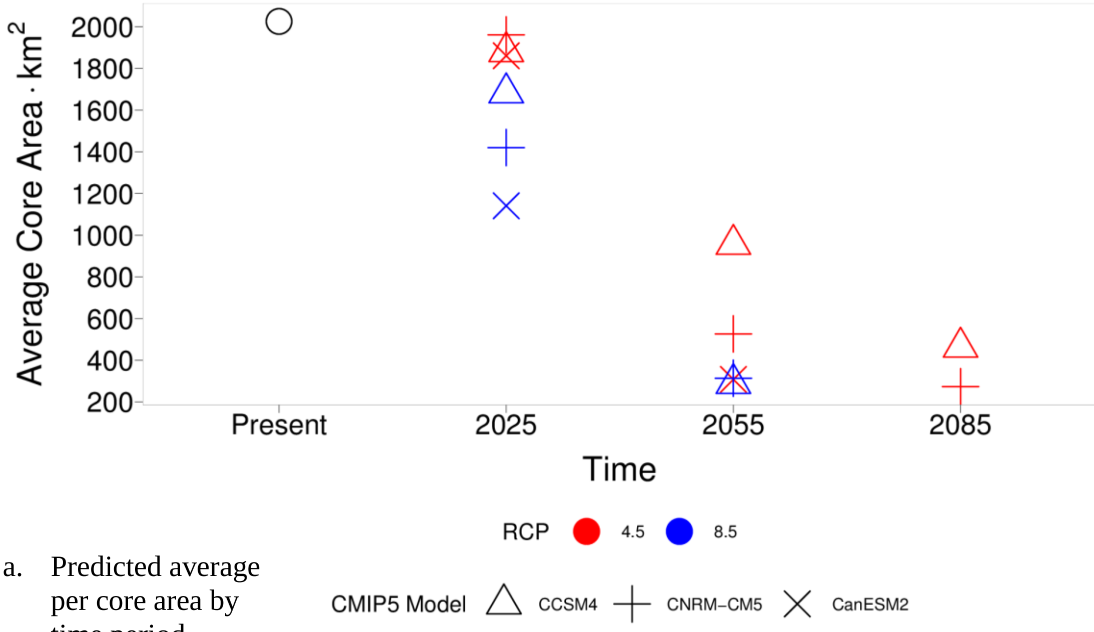


a. Predicted total core area by time period

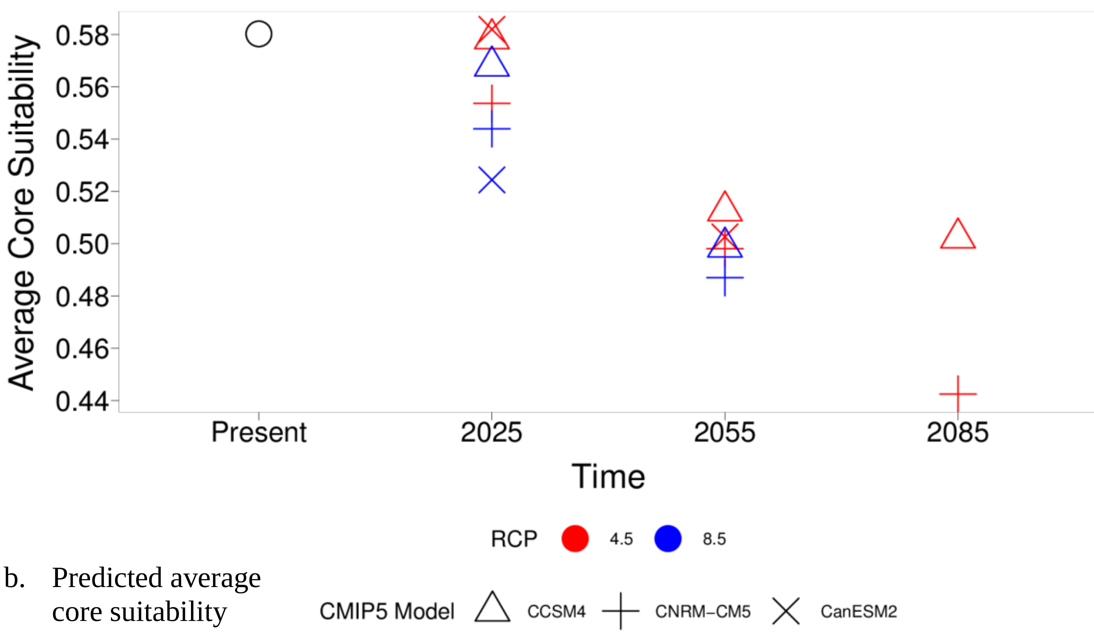


b. Predicted average total core area by CMIP5 model

Figure 3.2. Predicted total area of suitable *Lynx canadensis* habitat cores by time period and climate scenario. Plots depict (a) the total core area for each time period, Coupled Model Intercomparison Project Phase 5 (CMIP5) model, and Representative Concentration Pathway (RCP), and (b) the average total core area by CMIP5 model and RCP.

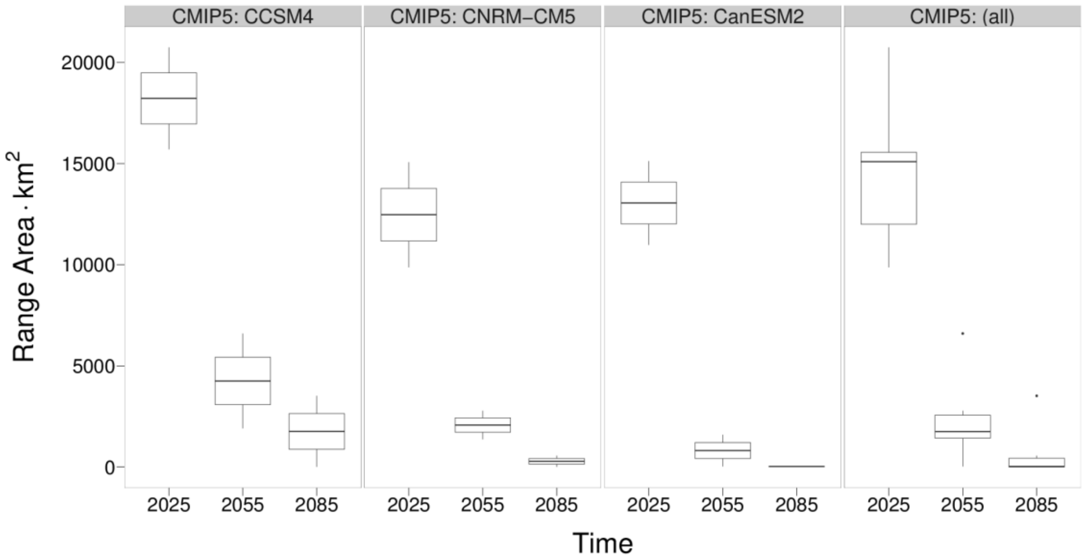


a. Predicted average per core area by time period

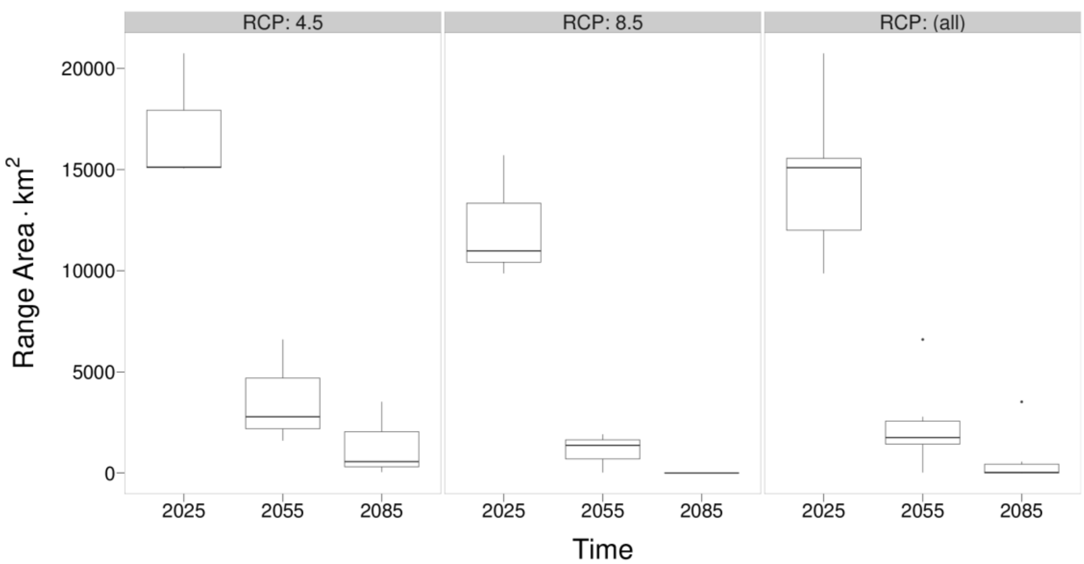


b. Predicted average core suitability by time period

Figure 3.3. Predicted per core area and suitability of *Lynx canadensis* habitat cores by time period and climate scenario. Plots depict (a) the average per core area for each time period, Coupled Model Intercomparison Project Phase 5 (CMIP5) model, and Representative Concentration Pathway (RCP), and (b) the average core suitability for each time period, CMIP5 model, and RCP.

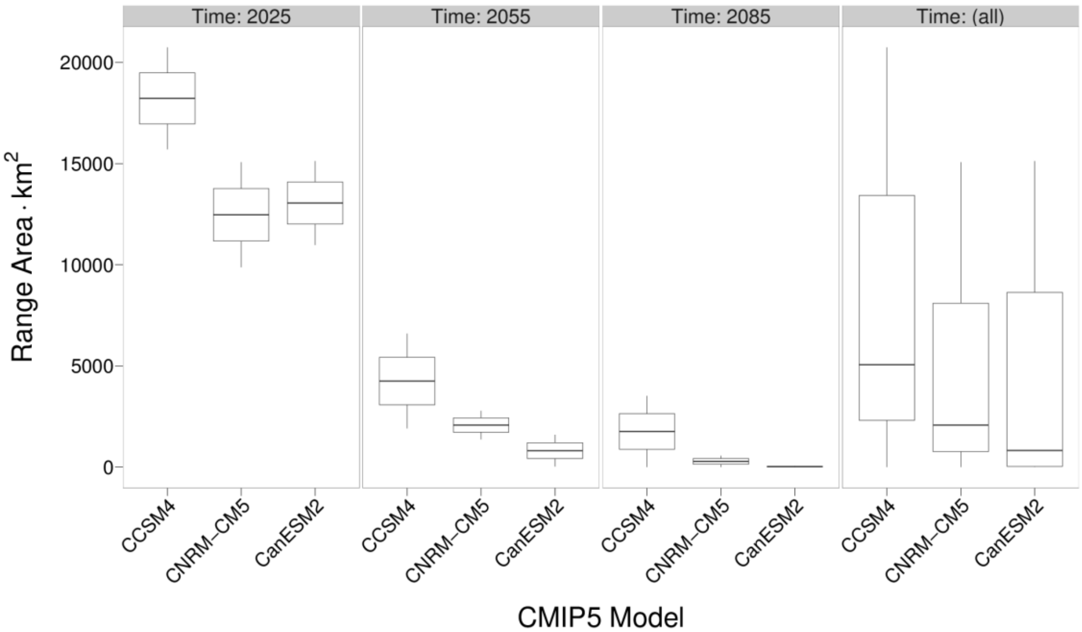


a. Distribution in range area by time period for each CMIP5 model

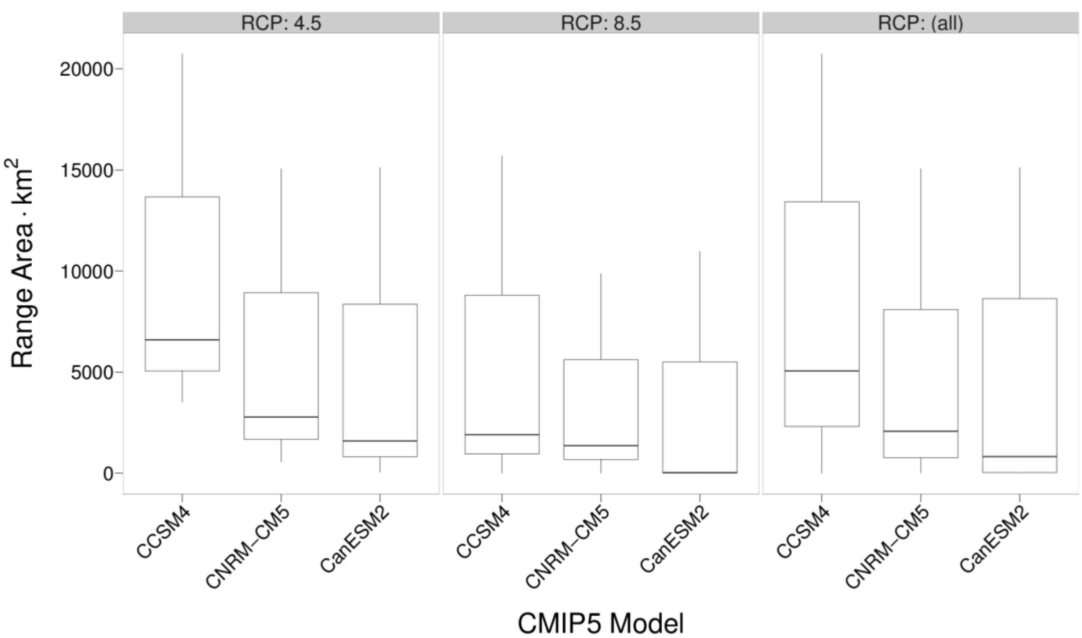


b. Distribution in range area by time period for each RCP

Figure 3.4. Side-by-side boxplots of predicted *Lynx canadensis* range area by time period. Each boxplot shows (a) the distribution in range area by time period (i.e. 2020s, 2050s, and 2080s) for each Coupled Model Intercomparison Project Phase 5 (CMIP5) model (i.e. CCSM4, CNRM-CM5, and CanESM2) and for all CMIP5 models and Representative Concentration Pathways (RCPs) combined, and (b) the distribution in range area by time period for each RCP (i.e. 4.5 and 8.5) and for all RCPs and CMIP5 models combined.

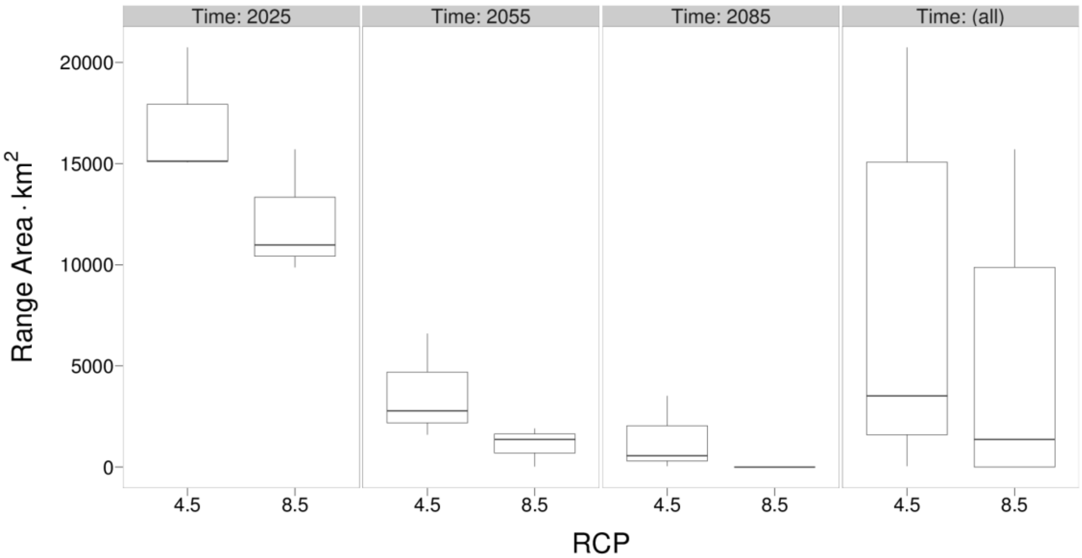


a. Distribution in range area by CMIP5 model for each time period

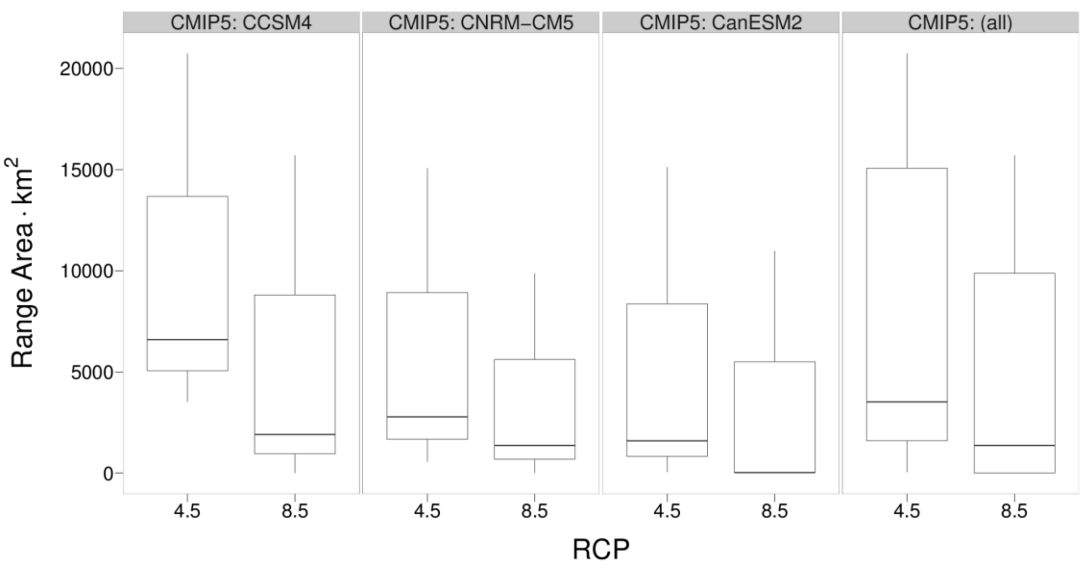


b. Distribution in range area by CMIP5 model for each RCP

Figure 3.5. Side-by-side boxplots of predicted *Lynx canadensis* range area by CMIP5 model. Each boxplot shows (a) the distribution in range area by Coupled Model Intercomparison Project Phase 5 (CMIP5) model (i.e. CCSM4, CNRM-CM5, and CanESM2) for each time period (i.e. 2020s, 2050s, and 2080s) and for all time periods and Representative Concentration Pathways (RCPs) combined, and (b) the distribution in range area by CMIP5 model for each RCP (i.e. 4.5 and 8.5) and for all RCPs and time periods combined.



a. Distribution in range area by RCP for each time period



b. Distribution in range area by RCP for each CMIP5 model

Figure 3.6. Side-by-side boxplots of predicted *Lynx canadensis* range area by RCP. Each boxplot panel shows (a) the distribution in range area by Representative Concentration Pathway (i.e. RCPs 4.5. and 8.5) for each time period (i.e. 2020s, 2050s, 2080s) and for all time periods and Coupled Model Intercomparison Project Phase 5 (CMIP5) models combined, and (b) the distribution in range area by RCP for each CMIP5 model (i.e. CCSM4, CNRM-CM5, and CanESM2) and for all CMIP5 models and time periods combined.

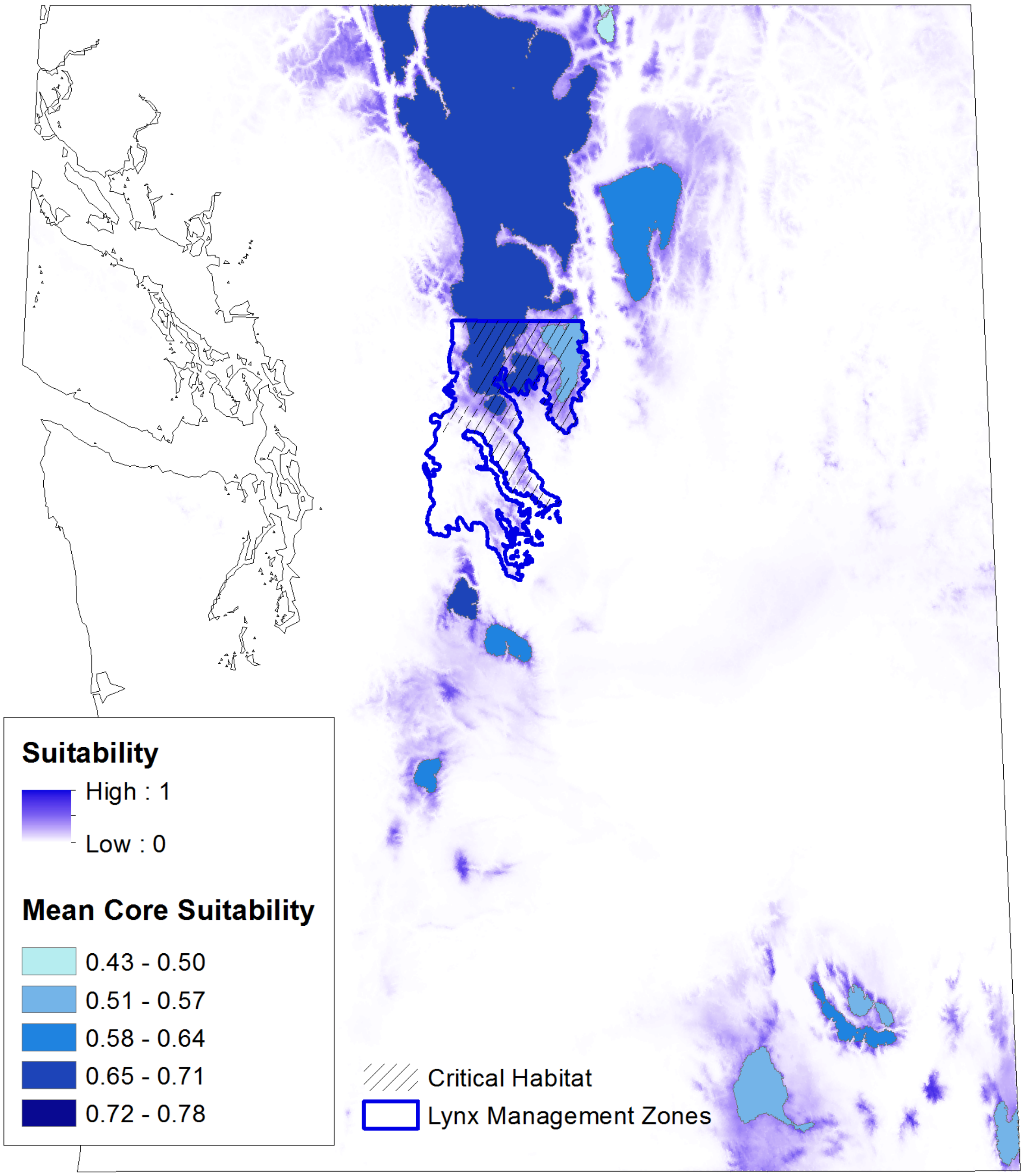


Figure 3.7. Projection map of *Lynx canadensis* habitat suitability and core areas for the present day. Core areas (solid colors) are superimposed over the gradient of projected habitat suitability. Lynx critical habitat (hatch) and the Okanogan Lynx Management Zone (blue outline) are shown for comparison.

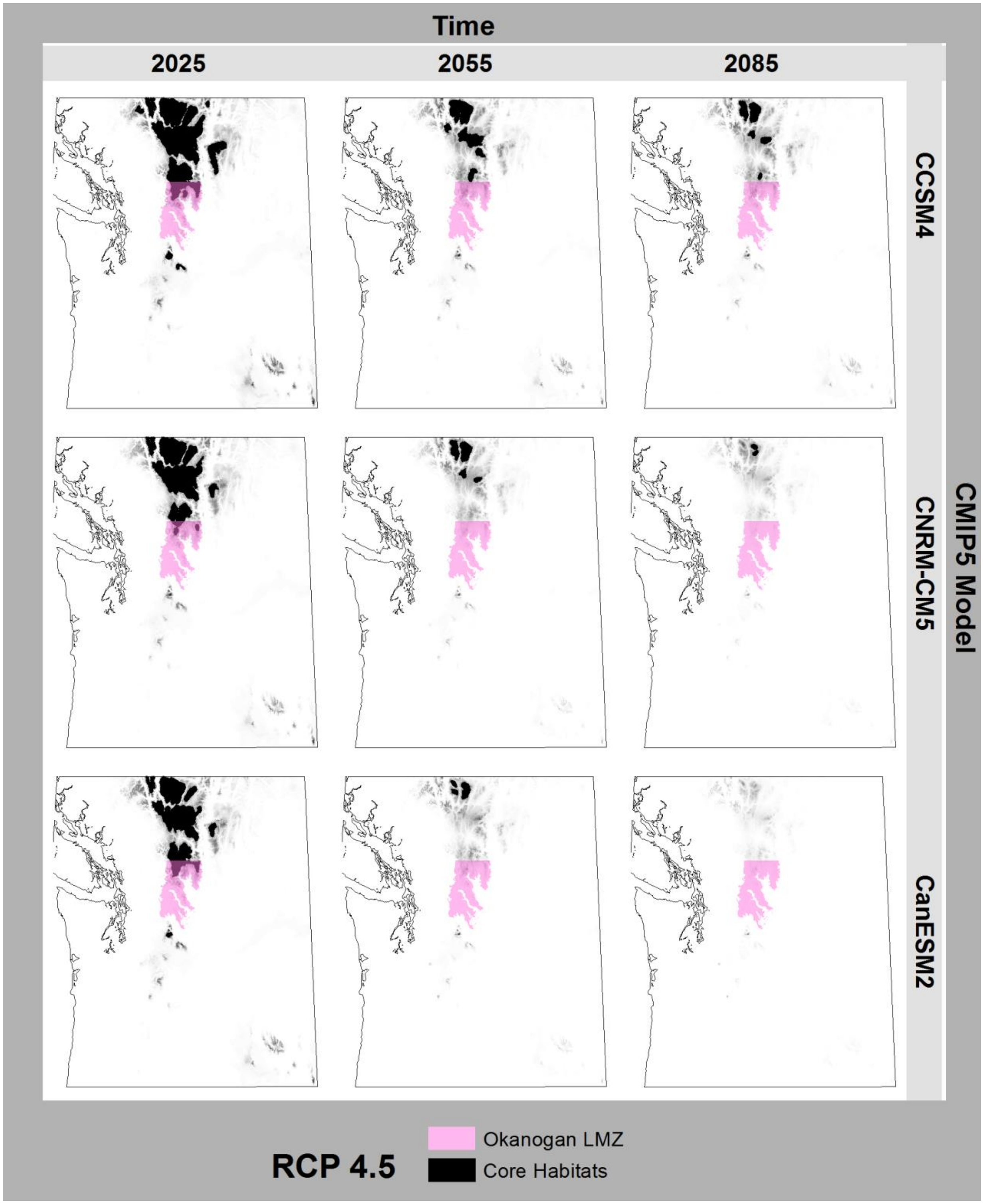


Figure 3.8. Projection maps of *Lynx canadensis* habitat suitability and core areas under climate futures for the Representative Concentration Pathway (RCP) 4.5. Projected core areas (solid black) are superimposed over a gradient of habitat suitability (white, 0; black, 1). The Okanogan Lynx Management Zone (LMZ; pink) is shown for comparison. CMIP5 = Coupled Model Intercomparison Project Phase 5.

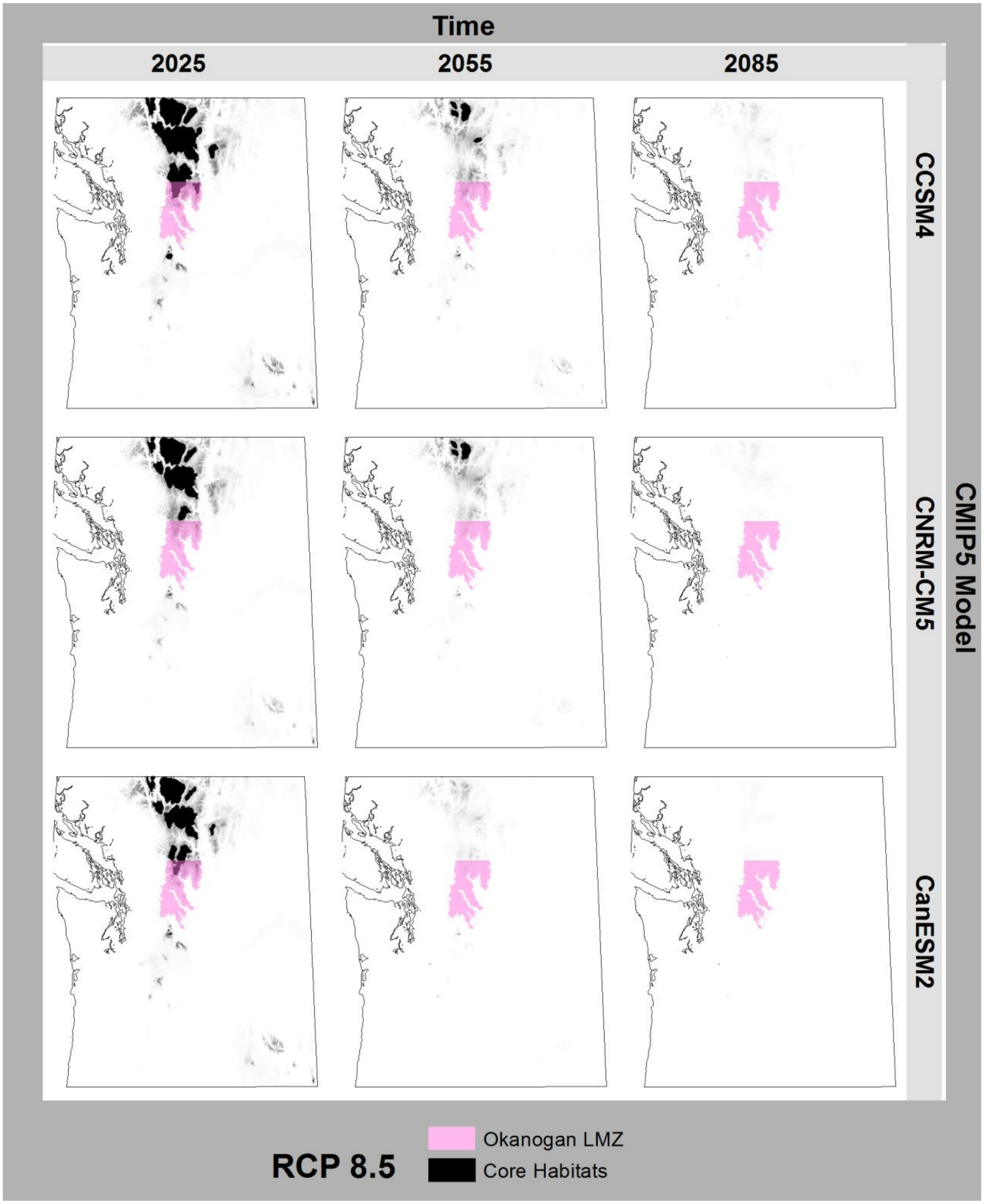


Figure 3.9. Projection maps of *Lynx canadensis* habitat suitability and core areas under climate futures for the Representative Concentration Pathway (RCP) 8.5. Projected core areas (solid black) are superimposed over a gradient of habitat suitability (white, 0; black, 1). The Okanogan Lynx Management Zone (LMZ; pink) is shown for comparison. CMIP5 = Coupled Model Intercomparison Project Phase 5.

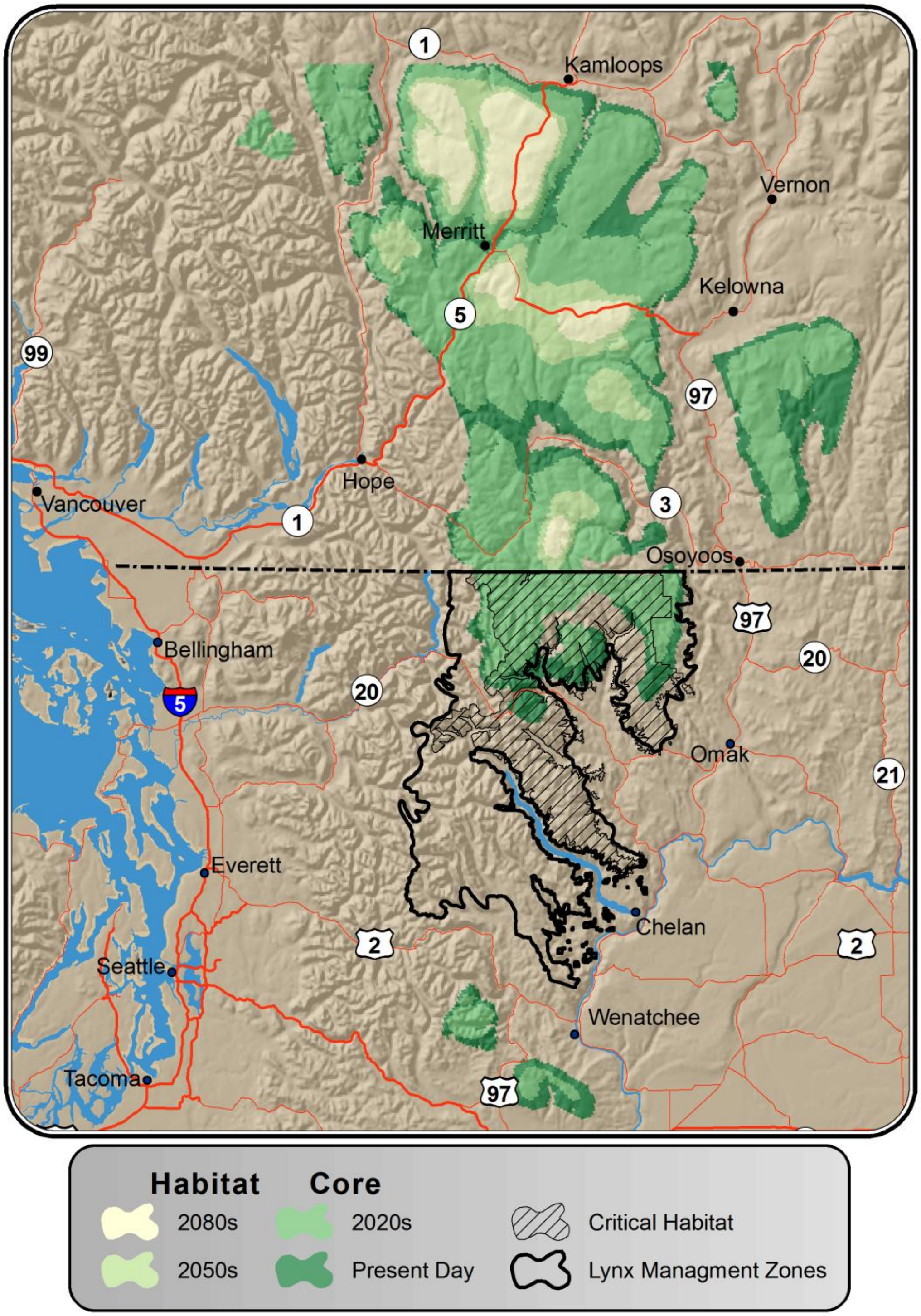


Figure 3.10. Map of the maximum extent of all *Lynx canadensis* core-habitat areas under all climate futures through time. Projected core areas (shades of green) represent the maximum extent of core areas under all climate scenarios for each time period (i.e. present, 2020s, 2050s, and 2080s). The Okanogan Lynx Management Zone (LMZ) and lynx critical habitat are shown for comparison. CMIP5 = Coupled Model Intercomparison Project Phase 5.

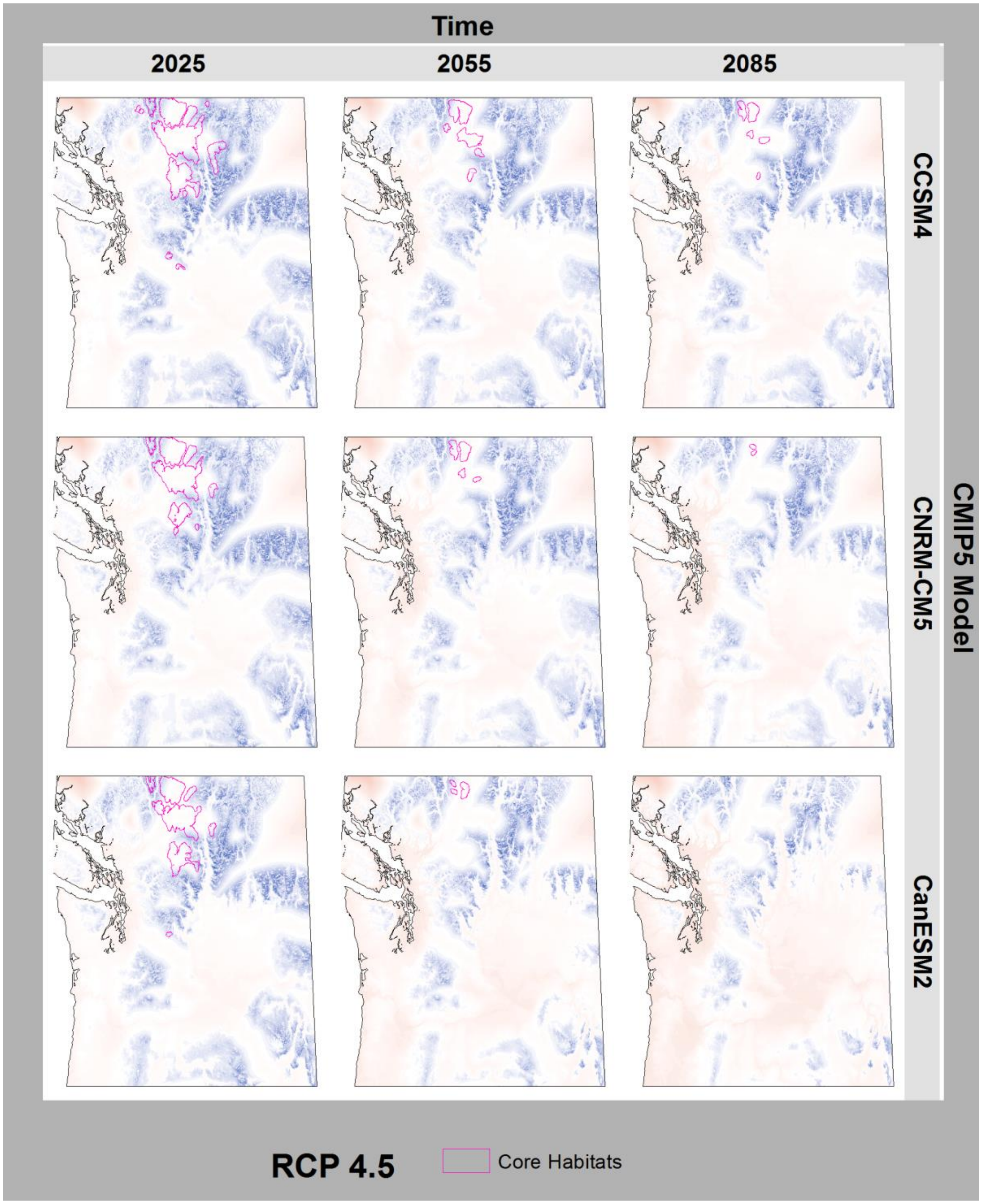


Figure 3.11. Multivariate environmental similarity surface (MESS) maps for future *Lynx canadensis* habitat suitability projections under Representative Concentration Pathway (RCP) 4.5. Projected core areas are shown for reference (pink outline). Positive values (blue) reflect low to no whereas negative values (red) reflect higher environmental novelty. Zero values (white) reflect differences with the median training space but with the range. More intense colors indicate greater magnitude. Maps are provided on the same scale (80 to -800) and are averaged across the 200 training subsamples. CMIP5 = Coupled Model Intercomparison Project Phase 5.

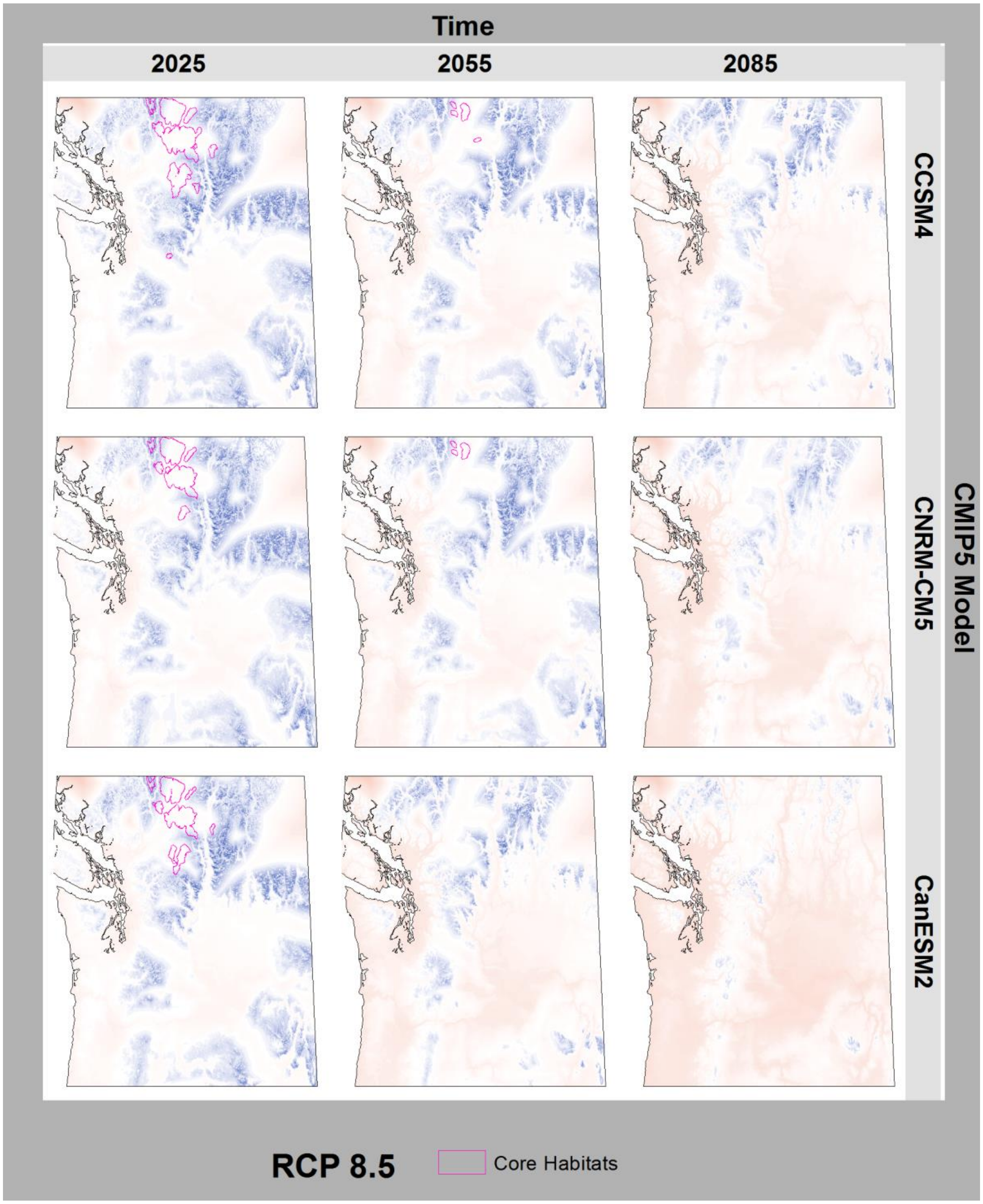


Figure 3.12. Multivariate environmental similarity surface (MESS) maps for future *Lynx canadensis* habitat suitability projections under Representative Concentration Pathway (RCP) 8.5. Projected core areas are shown for reference (pink outline). Positive values (blue) reflect low to no whereas negative values (red) reflect higher environmental novelty. Zero values (white) reflect differences with the median training space but with the range. More intense colors indicate greater magnitude. Maps are provided on the same scale (80 to -800) and are averaged across the 200 training subsamples. CMIP5 = Coupled Model Intercomparison Project Phase 5.

APPENDICES

APPENDIX A: LIST OF PREDICTORS USED IN SUITABILITY MODELING

Predictor Name	Abbreviation	Var. Type	Prox. Set	Full Set
Aspect	aspect	con	yes	yes
Maximum MTBS Burn Severity (1984-2013)	burn_severity	cat	yes	yes
Compound Topographic Index	topo_index	con	yes	yes
Distance to Local Roads (m)	local_roads	con	yes	yes
Distance to Primary Roads (m)	prmry_roads	con	yes	yes
Distance to Secondary Roads (m)	scndry_roads	con	yes	yes
Slope (°)	slope	con	yes	yes
Mean April 1 Snow Water Equivalent (mm) (1976-2005)	april1_swe	con	yes	yes
Modal MC2 Potential Vegetation Type (1981-2010)	vegtype	cat	yes	yes
ClimateWNA 1981-2010 Climate Normals – Annual Variables				
Hargreaves climatic moisture deficit (mm)	Hargr_CMD_annual	con	yes	yes
degree-days below 0°C (chilling degree-days)	dd0_annual	con	yes	yes
degree-days above 5°C (growing degree-days)	dd5_annual	con	yes	yes
frost-free period	frost_free_period	con	yes	yes
mean annual summer (May to Sept.) precipitation (mm)	msprecip_summer	con	yes	yes
mean warmest month temperature (°C)	tmean_warmest_month	con	yes	yes
mean annual temperature (°C)	tmean_annual	con	no	yes
summer heat-moisture index ((MWMT)/(MSP/1000))	hmi_summer	con	no	yes
annual heat-moisture index (MAT+10)/(MAP/1000))	hmi_annual	con	no	yes
the day of the year on which FFP begins	begin_frost_free	con	no	yes
degree-days below 18°C (heating degree-days)	dd_18_annual	con	no	yes

Predictor Name	Abbreviation	Var. Type	Prox. Set	Full Set
degree-days above 18°C (cooling degree-days)	dd18_annual	con	no	yes
the day of the year on which FFP ends	end_frost_free	con	no	yes
extreme minimum temperature over 30 years	tmin_extreme_30yr	con	no	yes
Hargreaves reference evaporation (mm)	Hargr_revap_annual	con	no	yes
extreme maximum temperature over 30 years	tmax_extreme_30yr	con	no	yes
mean annual precipitation (mm)	pmean_annual	con	no	yes
mean annual solar radiation (MJ m^{-2} d^{-1})	radiation_annual	con	no	yes
mean coldest month temperature (°C)	tmean_coldest_month	con	no	yes
the number of frost-free days	frost_free_days	con	no	yes
precipitation as snow (mm) between August in previous year and July in current year	snow_aug_july	con	no	yes
mean annual relative humidity (%)	rhmean_annual	con	no	yes
temperature difference between MWMT and MCMT, or continentality (°C)	temp_diff	con	no	yes
ClimateWNA 1981-2010 Climate Normals – Seasonal Variables				
winter degree-days below 0°C	dd0_winter	con	no	yes
summer degree-days above 5°C	dd5_summer	con	no	yes
spring degree-days above 5°C	dd5_spring	con	no	yes
summer number of frost-free days	frost_free_summer	con	no	yes
spring number of frost-free days	frost_free_spring	con	no	yes
summer mean temperature (°C)	tmean_summer	con	no	yes
winter mean temperature (°C)	tmean_winter	con	no	yes
summer mean maximum temperature (°C)	tmax_summer	con	no	yes
winter mean maximum temperature (°C)	tmax_winter	con	no	yes
summer mean minimum temperature (°C)	tmin_summer	con	no	yes

Predictor Name	Abbreviation	Var. Type	Prox. Set	Full Set
winter mean minimum temperature (°C)	tmin_winter	con	no	yes
autumn Hargreaves climatic moisture deficit (mm)	Hargr_CMD_autumn	con	no	yes
summer Hargreaves climatic moisture deficit (mm)	Hargr_CMD_summer	con	no	yes
spring Hargreaves climatic moisture deficit (mm)	Hargr_CMD_spring	con	no	yes
winter Hargreaves climatic moisture deficit (mm)	Hargr_CMD_winter	con	no	yes
autumn degree-days below 0°C	dd0_autumn	con	no	yes
summer degree-days below 0°C	dd0_summer	con	no	yes
spring degree-days below 0°C	dd0_spring	con	no	yes
autumn degree-days below 18°C	dd_18_autumn	con	no	yes
summer degree-days below 18°C	dd_18_summer	con	no	yes
spring degree-days below 18°C	dd_18_spring	con	no	yes
winter degree-days below 18°C	dd_18_winter	con	no	yes
autumn degree-days above 18°C	dd18_autumn	con	no	yes
summer degree-days above 18°C	dd18_summer	con	no	yes
spring degree-days above 18°C	dd18_spring	con	no	yes
winter degree-days above 18°C	dd18_winter	con	no	yes
autumn degree-days above 5°C	dd5_autumn	con	no	yes
winter degree-days below 5°C	dd5_winter	con	no	yes
autumn Hargreaves reference evaporation (mm)	Hargr_revap_autumn	con	no	yes
summer Hargreaves reference evaporation (mm)	Hargr_revap_summer	con	no	yes
spring Hargreaves reference evaporation (mm)	Hargr_revap_spring	con	no	yes
winter Hargreaves reference evaporation (mm)	Hargr_revap_winter	con	no	yes
autumn number of frost-free days	frost_free_autumn	con	no	yes
winter number of frost-free days	frost_free_winter	con	no	yes

Predictor Name	Abbreviation	Var. Type	Prox. Set	Full Set
autumn precipitation as snow (mm)	snow_autumn	con	no	yes
summer precipitation as snow (mm)	snow_summer	con	no	yes
spring precipitation as snow (mm)	snow_spring	con	no	yes
winter precipitation as snow (mm)	snow_winter	con	no	yes
autumn precipitation (mm)	precip_autumn	con	no	yes
summer precipitation (mm)	precip_summer	con	no	yes
spring precipitation (mm)	precip_spring	con	no	yes
winter precipitation (mm)	precip_winter	con	no	yes
autumn solar radiation (MJ m^{-2} d^{-1})	radiation_autumn	con	no	yes
summer solar radiation (MJ m^{-2} d^{-1})	radiation_summer	con	no	yes
spring solar radiation (MJ m^{-2} d^{-1})	radiation_spring	con	no	yes
winter solar radiation (MJ m^{-2} d^{-1})	radiation_winter	con	no	yes
autumn relative humidity (%)	humidity_autumn	con	no	yes
summer relative humidity (%)	humidity_summer	con	no	yes
spring relative humidity (%)	humidity_spring	con	no	yes
winter relative humidity (%)	humidity_winter	con	no	yes
autumn mean temperature (°C)	tmean_autumn	con	no	yes
spring mean temperature (°C)	tmean_spring	con	no	yes
autumn mean maximum temperature (°C)	tmax_autumn	con	no	yes
spring mean maximum temperature (°C)	tmax_spring	con	no	yes
autumn mean minimum temperature (°C)	tmin_autumn	con	no	yes
spring mean minimum temperature (°C)	tmin_spring	con	no	yes

APPENDIX B: PREPARATION OF ENVIRONMENTAL DATA

For all processing of environmental layers, I used the ArcGIS 10.3 (ESRI 2014) and the R language and environment (R Core Team 2013). All rasters were converted to file geodatabase objects and all were clipped to the projection area, reprojected from their original coordinate systems to the North America Albers Equal Area Conic projected coordinate system (PCS), resampled to a 1-km grid-cell size in one step, and snapped to a 1-km digital elevation model (DEM) (see *Topographic Variables*). I used the ArcGIS Extract by Mask tool with all environmental layers with extent of the projection area as a mask to ensure all extents were identical (required for MAXENT modeling). When processing was complete, I exported all file geodatabase rasters to the asci raster grids file format required for MAXENT modeling using the ArcGIS Raster to ASCII tool.

Study and Projection Area

As a baseline for both the study area polygon and the projection area mask, I created a new rectangular polygon in the North America Albers Equal Area Conic PCS that roughly matched the extent of the previously-prepared, 1-km DEM (see *Topographic Variables*), extending the projection area roughly 200 km north of the Washington-British Columbia (BC) border to include habitats from which lynx may migrate into Washington State. As movements in the northern parts of the range of greater than 100 km are considered characteristic for lynx and Fortin and Dale (2005) recommend an extent that is two to five times larger than the largest process being studied, a spatial extent extending 200 km into BC is appropriate for this analysis. I also extended the polygon into neighboring states as far as DEM values were available. I used this projection area polygon to clip all environmental data to the same extent.

For the study area polygon, which was strictly used to create maps of the projections for the figures, I used this extent as a mask to extract DEM values and reclassified all values equal to or less than zero as zero and all values greater than zero as one. I then converted the resulting map into a polygon. Although selecting an elevation threshold of zero for the extent may exclude some land grid cells at or below sea level near the coasts, I judged this acceptable because the focus of this analysis is on inland habitat suitability and lynx use of coastal areas is minimal. The resulting polygon matched existing distinctions between land and sea well and no grid cells at any significant distance from coastal areas were excluded.

Topographic Variables

Compound topographic index, slope, and aspect were derived from 1 arc-second digital elevation models (DEMs) from the U.S. Geological Survey National Elevation Dataset (NED). The DEMs were downloaded using the TNM Download Manager, mosaicked together with the ArcGIS Mosaic to New Raster tool as a 32-bit floating-point raster, and then, in one step, reprojected to the North America Albers Equal Area Conic PCS and resampled to a cell size of 1 km using the bilinear resampling technique.

To build the compound topographic index variable, I applied the Compound Topographic Index tool in the ArcGIS Geomorphometry and Gradient Metrics toolbox (version 2.0) (Evans et al. 2014) to the 1-km DEM. I generated the slope variable using the ArcGIS Spatial Analyst Slope tool applied to the 1-km DEM, using degrees as the unit of measurement. Similarly, I generated the aspect variable using the ArcGIS Spatial Analyst Aspect tool, also applied to the 1-km DEM.

External Data Sources Used:

- Layer: USGS National Elevation Dataset (NED) 1 arc-second ArcGrid
  - Source: U.S. Geological Survey
  - Variable: Elevation
  - Format: Raster
  - Cell Size: 1 arc-second
  - Original Projection: NAD 1983
  - Units of Measure: Meters
  - Publication Date: 2013
  - URLs:
    - http://nationalmap.gov/viewer.html
    - http://viewer.nationalmap.gov/apps/download_manager/

Maximum 30-Year Burn Severity

I downloaded 1984 to 2013 Monitoring Trends and Burn Severity (MTBS) National MTBS Burn Severity Mosaics from the MTBS data access website (Eidenshink et al. 2007). I clipped all rasters to the projection area and then reprojected them to the North America Albers Equal Area Conic PCS using the nearest resampling technique (data were categorical). I used the ArcGIS Raster Catalog to Raster Dataset tool to create a new raster that selected maximum values where cells overlapped from the original 30 rasters. Finally, I resampled the raster to a cell size of 1 km using the nearest resampling technique and snapped it to the 1-km DEM.

All burn severity classes were used, including those indicative of areas that could not be processed (class 6) and areas with increased greenness and vegetation response (class 5). Thematic classifications are based on a fire-related change map produced by differencing Normalized Burn Ratio (NBR) between pre-fire and post-fire maps, which result from analyzing bands within Landsat Thematic Mapper images (Eidenshink et al. 2007). The Normalized Burn Severity method has been used in fire severity mapping efforts by the U.S. Geological Survey and the U.S. Forest Service since 2002 (Eidenshink et al. 2007). Classification of MTBS burn severity and the percentage of each class in the U.S. portion of the study area is as follows:

0: Background (93.2%)
1: Unburned/Underburned to Low Burn Severity (1.5%)
2: Low Burn Severity (3.0%)
3: Moderate Burn Severity (1.4%)
4: High Burn Severity (0.7%)
5: Increased Greenness/Increased Vegetation Response (0.1%)
6: Non-Processing Area Mask (0.1%)

External Data Sources Used:

- Layer(s): CONUS Thematic Burn Severity Mosaics
    - Source: Monitoring Trends in Burn Severity (MTBS) Project
    - Variable: Burn Severity
    - Years Included: 1984-2013
    - Format: GeoTIFF
    - Cell Size: 30 m
    - Original Projections:
        - USA_Contiguous_Albers_Equal_Area_Conic_USGS_version
        - Albers_Conical_Equal Area
    - Publication Date: April 04, 2016
    - URLs:
        - http://mtbs.gov/dataaccess.html
        - http://mtbs.gov/nationalregional/download.html

Mean April 1 Snow Water Equivalent

I downloaded historical monthly day 1 Snow Water Equivalent (SWE) from 1950 to 2005 in netCDF file format from the Integrated Scenarios of the Future Northwest Environment data portal. Historical monthly SWE are outputs from a large-scale, semi-distributed hydrologic model called the Variable Infiltration Capacity (VIC) model, which simulates land-surface hydrology through incorporation of variable vegetation, soil types and topography (Liang et al. 1994). Historical outputs are based on the LIVNEH training dataset (Livneh et al. 2015) and are available for the first day of every month.

I developed an ArcGIS model that used the ArcGIS Make NetCDF Raster Layer tool and extracted the necessary layers of the NetCDF file (i.e. all April 1 measures of SWE from 1976 to 2005). I generated 30-year mean April 1 SWE from the extracted layers using the ArcGIS Cell

Statistics tool and reprojected the raster to the North America Albers Equal Area Conic PCS while also resampling to a 1-km grid-cell size using the bilinear resampling technique and snapping the layer to the 1-km DEM.

External Data Sources Used:

- Layer: Variable Infiltration Capacity (VIC) Monthly Day 1 Snow Water Equivalent (SWE)
    - Source: Integrated Scenarios of the Future Northwest Environment
    - Variable: SWE-monday1 (Snow Water Equivalent-Day 1)
    - Years Included: 1976-2005
    - Format: netCDF
    - Cell Size: ~6 km
    - Original Projection: WGS 1984
    - Publication Date: 2015
    - URL: http://climate.nkn.uidaho.edu/IntegratedScenarios/data_portal.php

Modal MC2 Potential Vegetation Type

I downloaded the historical yearly MC2 potential vegetation type dataset with fire suppression from 1981-2010 in netCDF file format from the Integrated Scenarios of the Future Northwest Environment data portal. Historical yearly vegetation type outputs are from the MC2 dynamic global vegetation model (DGVM), which simulates vegetation types, carbon fluxes, nitrogen and water, and wildfire (Lenihan et al. 1998, Bachelet et al. 2001, Sheehan et al. 2015). Historical outputs are based on upscaled historical Parameter-elevation Regressions on Independent Slopes Model (PRISM) data (Daly et al. 2008, Sheehan et al. 2015).

I developed an ArcGIS model that used the ArcGIS Make NetCDF Raster Layer tool and extracted the necessary layers of the NetCDF file (*v_type* from 1981 to 2010). I generated 30-year modal MC2 potential vegetation type by finding the modal vegetation types in the extracted layers from 1981-2010 using the ArcGIS Cell Statistics tool. I then reprojected the resulting raster to the North America Albers Equal Area Conic PCS while also resampling to a 1-km grid-cell size using the bilinear resampling technique and snapping the layer to the 1-km DEM. **Table B.1** provides the modal vegetation types identified within the study area.

External Data Sources Used:

- Layer: Yearly MC2 Potential Vegetation Type with Fire Suppression
    - Source: Integrated Scenarios of the Future Northwest Environment
    - Variable: V_TYPE (Vegetation Type)
    - Years Included: 1981-2010
    - Format: netCDF
    - Cell Size: 4 km
    - Original Projection: WGS 1984
    - Publication Date: 2015
    - URL: http://climate.nkn.uidaho.edu/IntegratedScenarios/data_portal.php

Table B.1. Modal MC2 potential vegetation types within the study area

Vegetation Type Number	Vegetation Type Class	Percentage of Study Area*
2	Tundra	0.10%
6	Subalpine	6.80%
7	Maritime Evergreen Needleleaf Forest	19.80%
8	Temperate Evergreen Needleleaf Forest	28.10%
10	Temperate Cool Mixed Forest	2.80%
12	Temperate Evergreen Needleleaf Woodland	26.50%
14	Temperate Cool Mixed Woodland	0.00%**
16	Temperate Shrubland	8.10%
17	Temperate Grassland	1.40%
27	Subtropical Shrubland	1.30%
28	Subtropical Grassland	0.80%
36	Cool Needleleaf Forest	4.20%

* MC2 potential vegetation type projections for 1981 – 2010 were only available within the continental United States. Thus percentages refer to only the U.S. portion of the study area.

** Value is beyond the precision specified.

Distance to Road Types

I used 2014 TIGER/Line roads (U.S. Census Bureau 2014) and Digital Road Atlas (DRA) Master Partially-Attributed Roads from the GeoBC data catalogue to generate all distance to road variables. I downloaded TIGER/Line shapefiles for all roads and all counties within the study area from the census File Transfer Protocol (FTP) website and DRA roads from the British Columbia government data catalogue. For TIGER/Line roads and DRA roads, I reprojected the shapefiles to the North America Albers Equal Area Conic PCS, ensuring shapes were preserved, and then merged shapefiles.

Using ArcGIS, I classified MAF/TIGER Feature Class Code (MTFCC) S1100 (generally divided, limited-access highways within the interstate highway system) and the BC road class (i.e. ROAD_CLASS) freeway as primary roads (i.e. freeways). I classified MTFCC S1200 (main arteries, usually in the U.S. Highway, State Highway or County Highway system) and the BC road classes highway, arterial, and collector as secondary roads (i.e. highways). For local roads, I used MTFCCs S1400 (local neighborhood road, rural road, and city street), S1500 (vehicular trail), S1640 (service drives), and S1740 (private roads) and BC road classes driveway, lane, local, recreation, resource, restricted, service, strata, unclassified. I excluded the following types from the final road shapefile: MTFCCs S1630 (ramp), S1710 (walkway/pedestrian trail), S1720 (stairway), S1730 (alley), S1750 (internal U.S. Census Bureau use), S1780 (parking lot road), and S1820 (bike path or trail) and the BC road classes alleyway, ferry, passenger, skid, pedestrian, trail, water, and ramp.

To create variables representative of distance to each type of road (i.e. primary, secondary, or local), I split the shapefile accordingly and used the ArcGIS Euclidean Distance tool to generate distance from roads for each road type, using a grid-cell size of 1 km and snapping the resulting raster to the 1-km DEM.

External Data Sources Used:

- Layer: 2014 TIGER/Line Shapefiles, All Roads
    - Source: U.S. Department of Commerce, U.S. Census Bureau, Geography Division
    - Format: Vector digital data
    - Mapping Scale: 1:100,000
    - Original Projection: NAD 1983
    - Publication Date: May 2014
    - FIPS county codes: Multiple in Washington, Idaho, and Oregon
    - URLs:
        - https://www.census.gov/cgi-bin/geo/shapefiles/index.php
        - http://www2.census.gov/geo/tiger/TIGER2014/ROADS/

- Layer: Digital Road Atlas (DRA) - Master Partially-Attributed Roads
    - Source: Ministry of Forests, Lands and Natural Resource Operations - GeoBC
    - Format: Vector digital data
    - Mapping Scale: 1:24,000
    - Original Projection: NAD_1983_BC_Environment_Albers
    - Publication Date: December 10, 2014
    - URL: https://catalogue.data.gov.bc.ca/dataset/digital-road-atlas-dra-master-partially-attributed-roads

Seasonal and Annual ClimateWNA Variables

I used the R package *SDMTools* version 1.1-221 (VanDerWal et al. 2014) to convert an ASCII version of the 1-km DEM to the comma separated value (CSV) file format for the ClimateWNA download application (Wang et al. 2012). ClimateWNA is a program that provides climate normal, annual, seasonal and monthly data for historical and future periods in western North America. The baseline and historical outputs are based on 800-m PRISM data (Daly et al. 2008) integrated with historical monthly data from the Climate Research Unit (CRU) (Harris et al. 2014). Climate data for the future periods included in this analysis (i.e. 2020s, 2050s, and 2080s) are from General Circulation Models (GCMs) of the Coupled Model Intercomparison Project

Phase 5 (CMIP5) included in the International Panel on Climate Change Fifth Assessment Report (IPCC 2014). Fifteen GCMs and two greenhouse gas emission scenarios (RCPs 4.5 and 8.5) are available. Downscaling is accomplished using a combination of bilinear interpolation and dynamic local elevational adjustment (Wang et al. 2012).

I downloaded annual and seasonal 1981-2010 Climate Normals and future climate data for RCPs 4.5 and 8.5 for three GCMs (CanESM2, CNRM-CM5, CCSM4) for all three time periods available from ClimateWNA v5.21 using the prepared elevation. I then converted the outputs to the asci raster grids file format using R, and then used ArcGIS to reproject all rasters to the North America Albers Equal Area Conic PCS, resample them to 1-km using the bilinear resampling technique, and snap them to the 1-km DEM.

External Data Sources Used:

- Layer: Yearly and Seasonal Climatic Variables
    - Source: ClimateWNA v5.21
    - Years Included:
        - 1981-2010
        - 2020s (2010-2039)
        - 2050s (2040-2069)
        - 2080s (2070-2099)
    - CMIP5 Models: CanESM2, CNRM-CM5, CCSM4
    - RCPs: 4.5 and 8.5
    - Format: CSV
    - Cell Size: 1 km (downscaled from 4 km)
    - Original Projection: WGS 1984
    - Publication Date: May 06, 2016
    - URL: http://cfcg.forestry.ubc.ca/projects/climate-data/climatebcwna/#ClimateWNA

Other Spatial Layers

Unit 4 of lynx critical habitat and Washington State Lynx Management Zones were used as reference polygons in projection maps.

- Layer: Unit 4 – North Cascades of Lynx Critical Habitat
    - Source: U.S. Fish and Wildlife Service
    - Format: Shapefile
    - Original Projection: WGS 1984
    - Publication Date: September 12, 2014
    - URL: https://www.fws.gov/mountain-prairie/es/canadaLynx.php

APPENDIX C: CORE AREA METRICS AND PROJECTIONS OF HABITAT SUITABILITY FOR EACH TIME PERIOD, CMIP5 MODEL, AND RCP

Table C.1. Mean count of core *Lynx canadensis* habitats within the study area aggregated by time periods and climate scenarios.

	Time	RCP	CMIP5 Model	Mean No.	n	SD	Min	Max
By Time Period	Present	NA	NA	13.00	1	NA	NA	NA
	2025	All	All	7.67	6	1.25	6	10
	2055	All	All	3.17	6	1.57	0	5
	2085	All	All	1.00	6	1.83	0	5
By RCP	Future	4.5	All	4.67	9	2.94	0	10
	Future	8.5	All	3.22	9	3.26	0	8
By CMIP5 Model	Future	All	CCSM4	5.33	6	3.14	0	10
	Future	All	CNRM-CM5	3.50	6	2.50	0	7
	Future	All	CanESM2	3.00	6	3.37	0	8
By CMIP5 Model and RCP	Future	4.5	CCSM4	6.67	3	2.36	5	10
	Future	4.5	CNRM-CM5	4.00	3	2.45	1	7
	Future	4.5	CanESM2	3.33	3	2.87	0	7
	Future	8.5	CCSM4	4.00	3	3.27	0	8
	Future	8.5	CNRM-CM5	3.00	3	2.45	0	6
	Future	8.5	CanESM2	2.67	3	3.77	0	8

NA = not applicable. RCP = Representative Concentration Pathway. CMIP5 = Coupled Model Intercomparison Project Phase 5.

Table C.2. Mean total core area of *Lynx canadensis* habitats within the study area aggregated by time periods and climate scenarios.

	Time	RCP	CMIP5 Model	Mean Area (km^2)	n	SD	Min	Max
By Time Period	Present	NA	NA	26340.00	1	NA	NA	NA
	2025	All	All	12781.33	6	3397	8524	18811
	2055	All	All	1650.67	6	1528	0	4780
	2085	All	All	430.83	6	847	0	2312
By RCP	Future	4.5	All	6218.22	9	6647	0	18811
	Future	8.5	All	3690.33	9	4910	0	13465
By CMIP5 Model	Future	All	CCSM4	6753.67	6	6964	0	18811
	Future	All	CNRM-CM5	4262.17	6	5125	0	13730
	Future	All	CanESM2	3847.00	6	5246	0	13029
By CMIP5 Model and RCP	Future	4.5	CCSM4	8634.33	3	7266	2312	18811
	Future	4.5	CNRM-CM5	5369.33	3	5959	273	13730
	Future	4.5	CanESM2	4651.00	3	5936	0	13029
	Future	8.5	CCSM4	4873.00	3	6094	0	13465
	Future	8.5	CNRM-CM5	3155.00	3	3816	0	8524
	Future	8.5	CanESM2	3043.00	3	4303	0	9129

NA = not applicable. RCP = Representative Concentration Pathway. CMIP5 = Coupled Model Intercomparison Project Phase 5.

Table C.3. Mean per core area of *Lynx canadensis* habitats within the study area.

	Time	RCP	CMIP5 Model	Mean Area (km^2)	n	SD	Min	Max
By Time Period*	Present	NA	NA	2026.15	13	4740.14	111	18298
	2025	All	All	1667.13	46	1997.88	101	8274
	2055	All	All	521.26	19	555.15	134	2312
	2085	All	All	430.83	6	300.92	112	974
By RCP*	Future	4.5	All	1332.48	42	1900.23	101	8274
	Future	8.5	All	1145.28	29	1436.83	129	5790
By CMIP5 Model*	Future	All	CCSM4	1266.31	32	1851.00	101	8274
	Future	All	CNRM-CM5	1217.76	21	1709.43	106	7156
	Future	All	CanESM2	1282.33	18	1510.67	120	5437
By CMIP5 Model and RCP*	Future	4.5	CCSM4	1295.15	20	1946.98	101	8274
	Future	4.5	CNRM-CM5	1342.33	12	1964.16	106	7156
	Future	4.5	CanESM2	1395.30	10	1716.93	120	5437
	Future	8.5	CCSM4	1218.25	12	1677.77	129	5790
	Future	8.5	CNRM-CM5	1051.67	9	1275.19	153	3857
	Future	8.5	CanESM2	1141.13	8	1189.15	176	3510

* Aggregated statistics are biased upward due to the absence of cores under high impact scenarios. NA = not applicable. RCP = Representative Concentration Pathway. CMIP5 = Coupled Model Intercomparison Project Phase 5.

Table C.4. Mean core suitability of *Lynx canadensis* habitats within the study area.

	Time	RCP	CMIP5 Model	Mean Suitability	n	SD	Min	Max
By Time Period*	Present	NA	NA	0.580	13	0.061	0.494	0.682
	2025	All	All	0.559	46	0.085	0.433	0.784
	2055	All	All	0.501	19	0.043	0.448	0.612
	2085	All	All	0.492	6	0.049	0.442	0.574
By RCP*	Future	4.5	All	0.542	42	0.083	0.433	0.784
	Future	8.5	All	0.533	29	0.073	0.447	0.732
By CMIP5 Model*	Future	All	CCSM4	0.544	32	0.078	0.453	0.784
	Future	All	CNRM-CM5	0.525	21	0.081	0.433	0.760
	Future	All	CanESM2	0.543	18	0.076	0.447	0.726
By CMIP5 Model and RCP*	Future	4.5	CCSM4	0.543	20	0.082	0.453	0.784
	Future	4.5	CNRM-CM5	0.526	12	0.088	0.433	0.760
	Future	4.5	CanESM2	0.558	10	0.073	0.463	0.726
	Future	8.5	CCSM4	0.545	12	0.071	0.468	0.732
	Future	8.5	CNRM-CM5	0.525	9	0.071	0.448	0.698
	Future	8.5	CanESM2	0.524	8	0.074	0.447	0.684

* Aggregated statistics are biased upward due to the absence of cores under high impact scenarios. Suitability is on a scale of 0.38 to 1. NA = not applicable. RCP = Representative Concentration Pathway. CMIP5 = Coupled Model Intercomparison Project Phase 5.

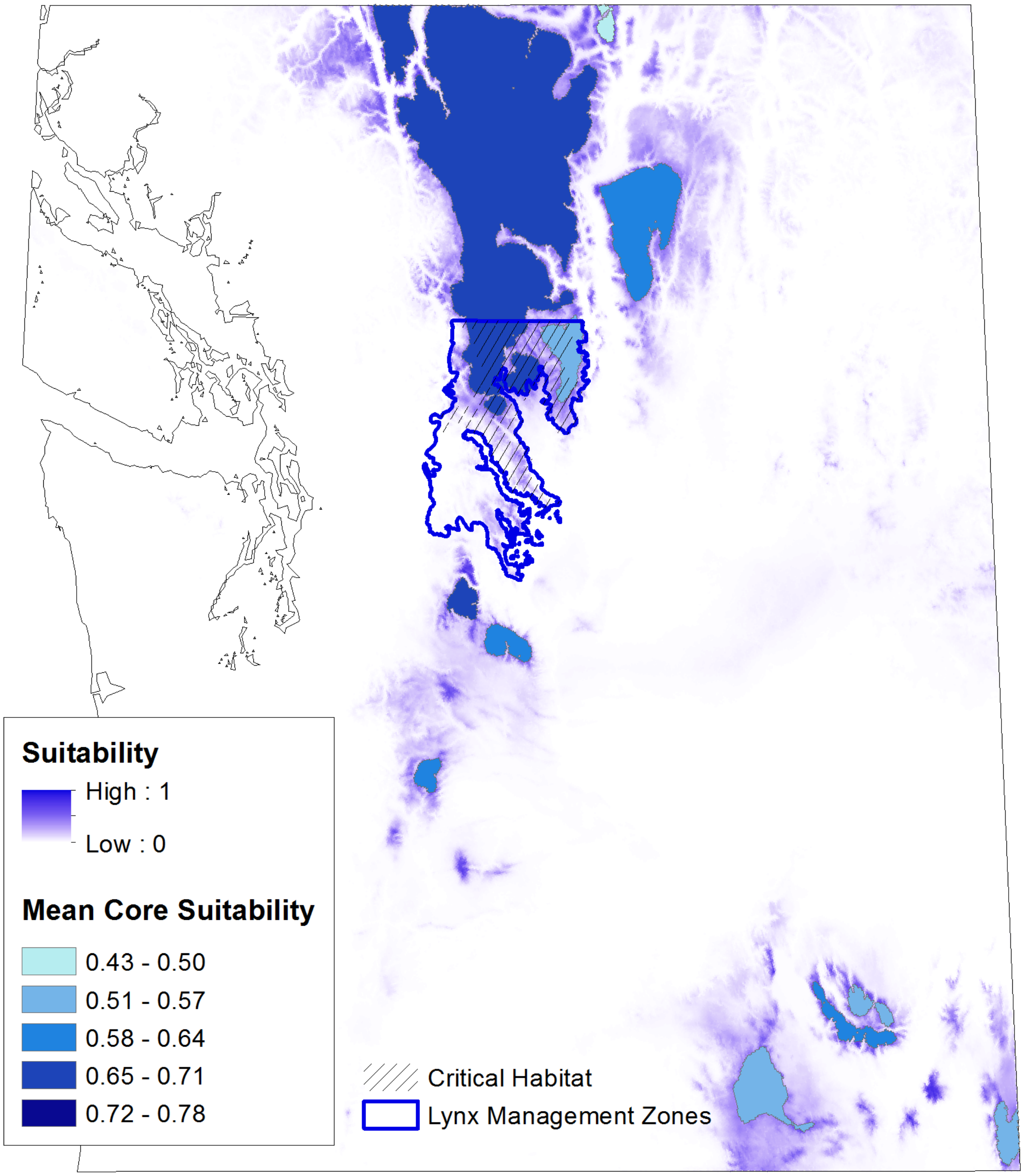


Figure C.1. Projection of *Lynx canadensis* habitat suitability and core habitat areas for the present day. Core areas (solid colors) are superimposed over the gradient of projected habitat suitability. Lynx critical habitat (hatch) and the Okanogan Lynx Management Zone (blue outline) are shown for comparison.

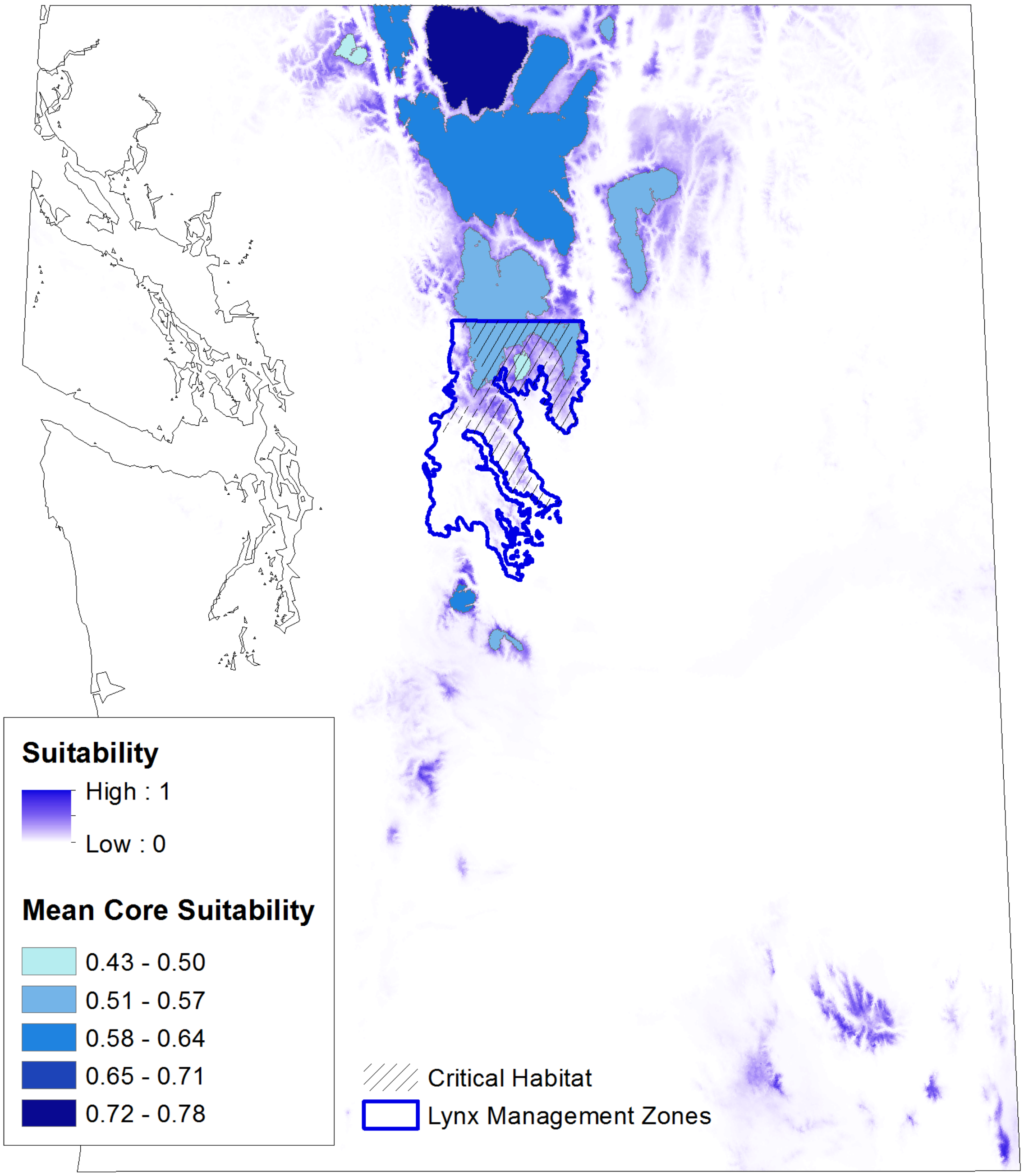


Figure C.2. Projection of *Lynx canadensis* habitat suitability and core areas for the 2020s under the CCSM4 RCP 4.5 climate scenario. Core areas (solid colors) are superimposed over the gradient of projected habitat suitability. Lynx critical habitat (hatch) and the Okanogan Lynx Management Zone (blue outline) are shown for comparison. RCP = Representative Concentration Pathway.

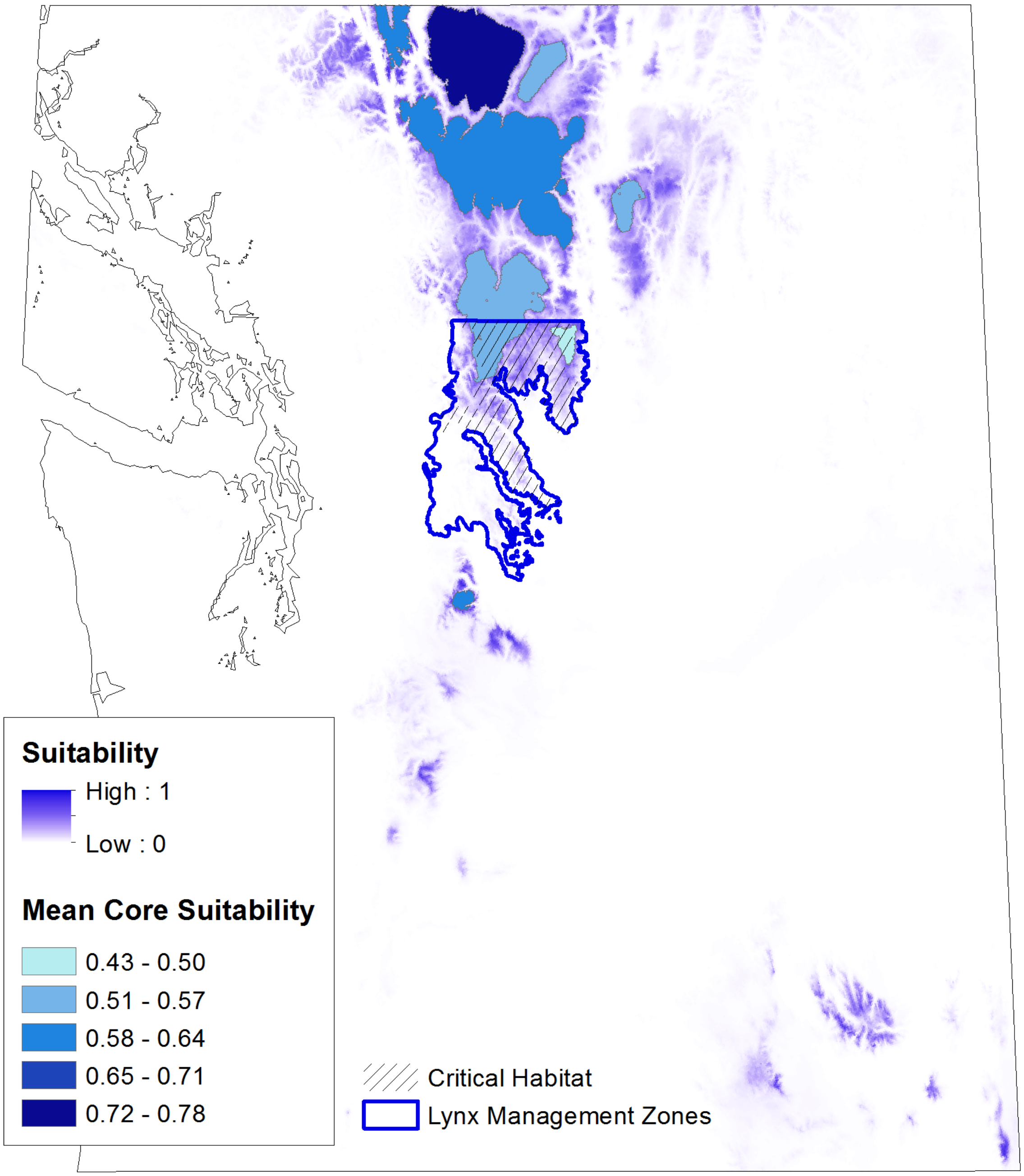


Figure C.3. Projection of *Lynx canadensis* habitat suitability and core areas for the 2020s under the CCSM4 RCP 8.5 climate scenario. Core areas (solid colors) are superimposed over the gradient of projected habitat suitability. Lynx critical habitat (hatch) and the Okanogan Lynx Management Zone (blue outline) are shown for comparison. RCP = Representative Concentration Pathway.

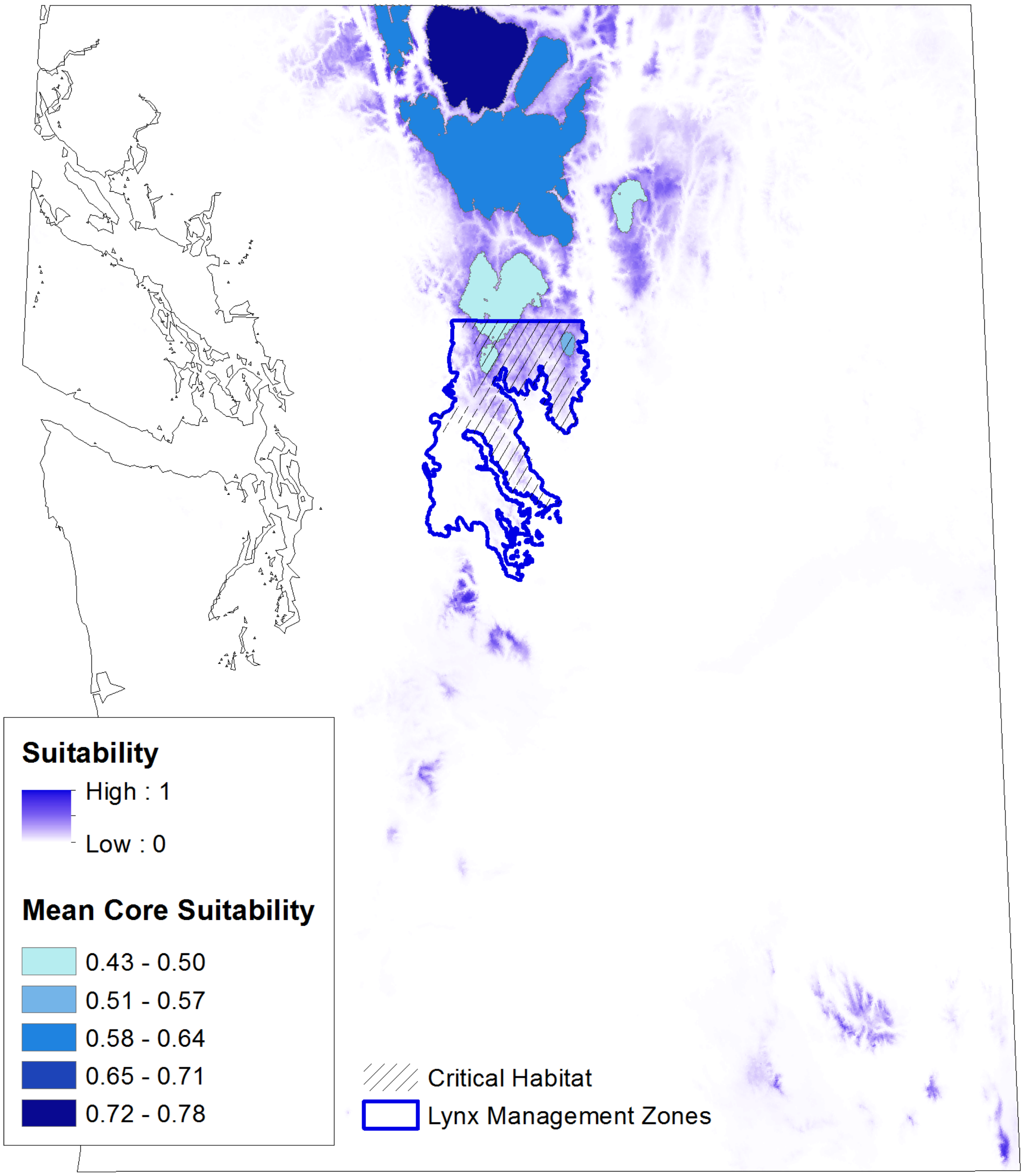


Figure C.4. Projection of *Lynx canadensis* habitat suitability and core areas for the 2020s under the CNRM-CM5 RCP 4.5 climate scenario. Core areas (solid colors) are superimposed over the gradient of projected habitat suitability. Lynx critical habitat (hatch) and the Okanogan Lynx Management Zone (blue outline) are shown for comparison. RCP = Representative Concentration Pathway.

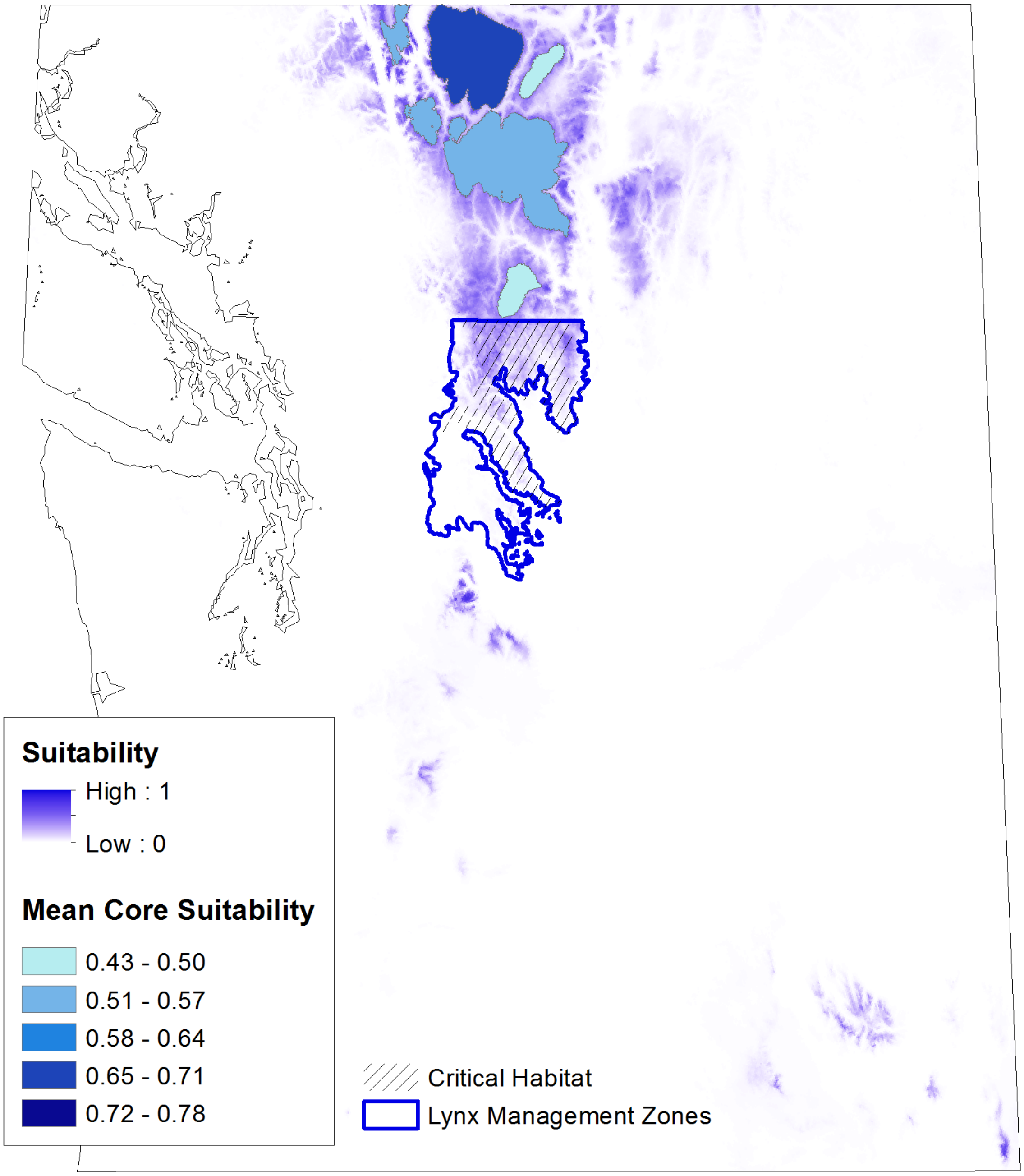


Figure C.5. Projection of *Lynx canadensis* habitat suitability and core areas for the 2020s under the CNRM-CM5 RCP 8.5 climate scenario. Core areas (solid colors) are superimposed over the gradient of projected habitat suitability. Lynx critical habitat (hatch) and the Okanogan Lynx Management Zone (blue outline) are shown for comparison. RCP = Representative Concentration Pathway.

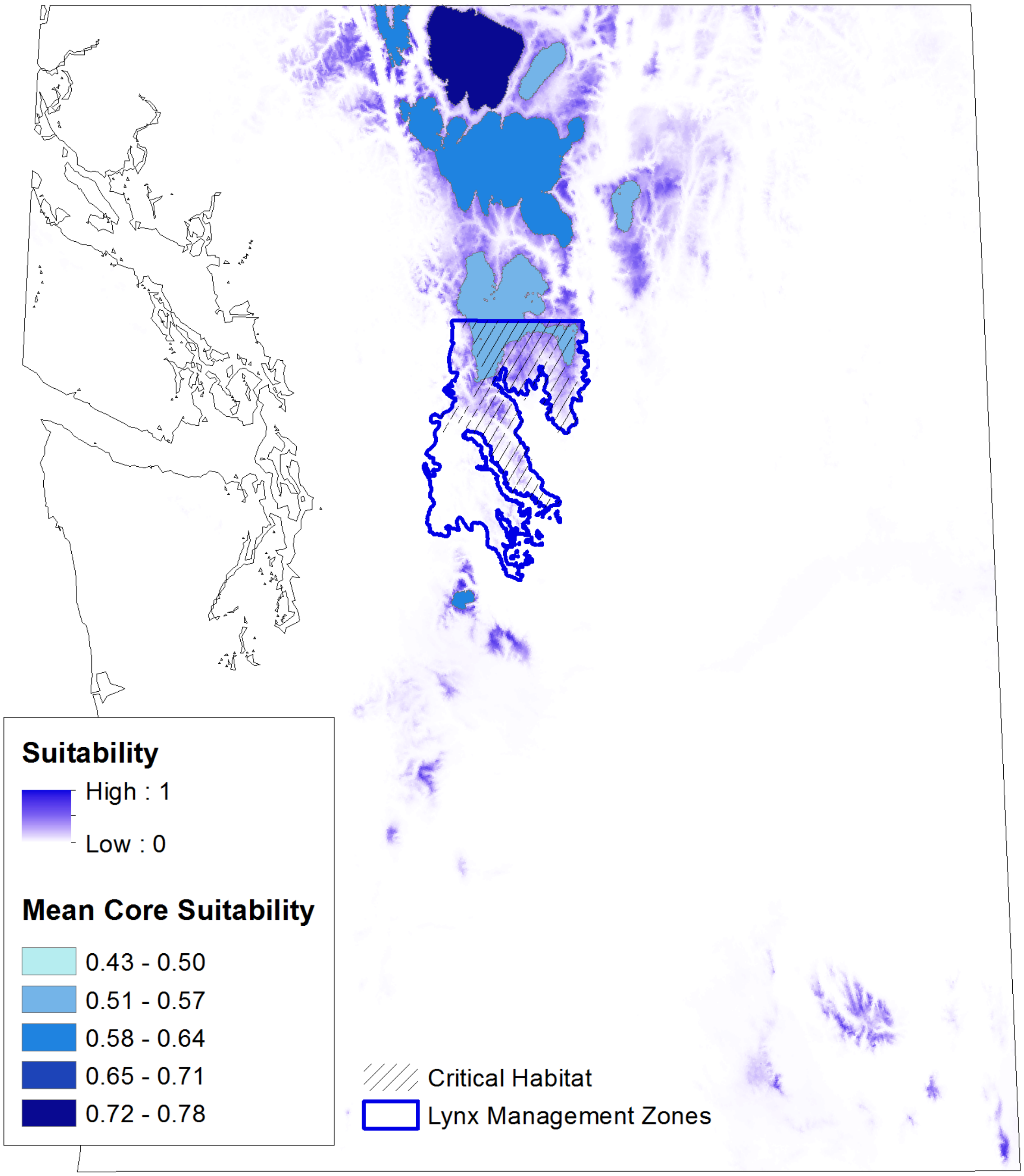


Figure C.6. Projection of *Lynx canadensis* habitat suitability and core areas for the 2020s under the CanESM2 RCP 4.5 climate scenario. Core areas (solid colors) are superimposed over the gradient of projected habitat suitability. Lynx critical habitat (hatch) and the Okanogan Lynx Management Zone (blue outline) are shown for comparison. RCP = Representative Concentration Pathway.

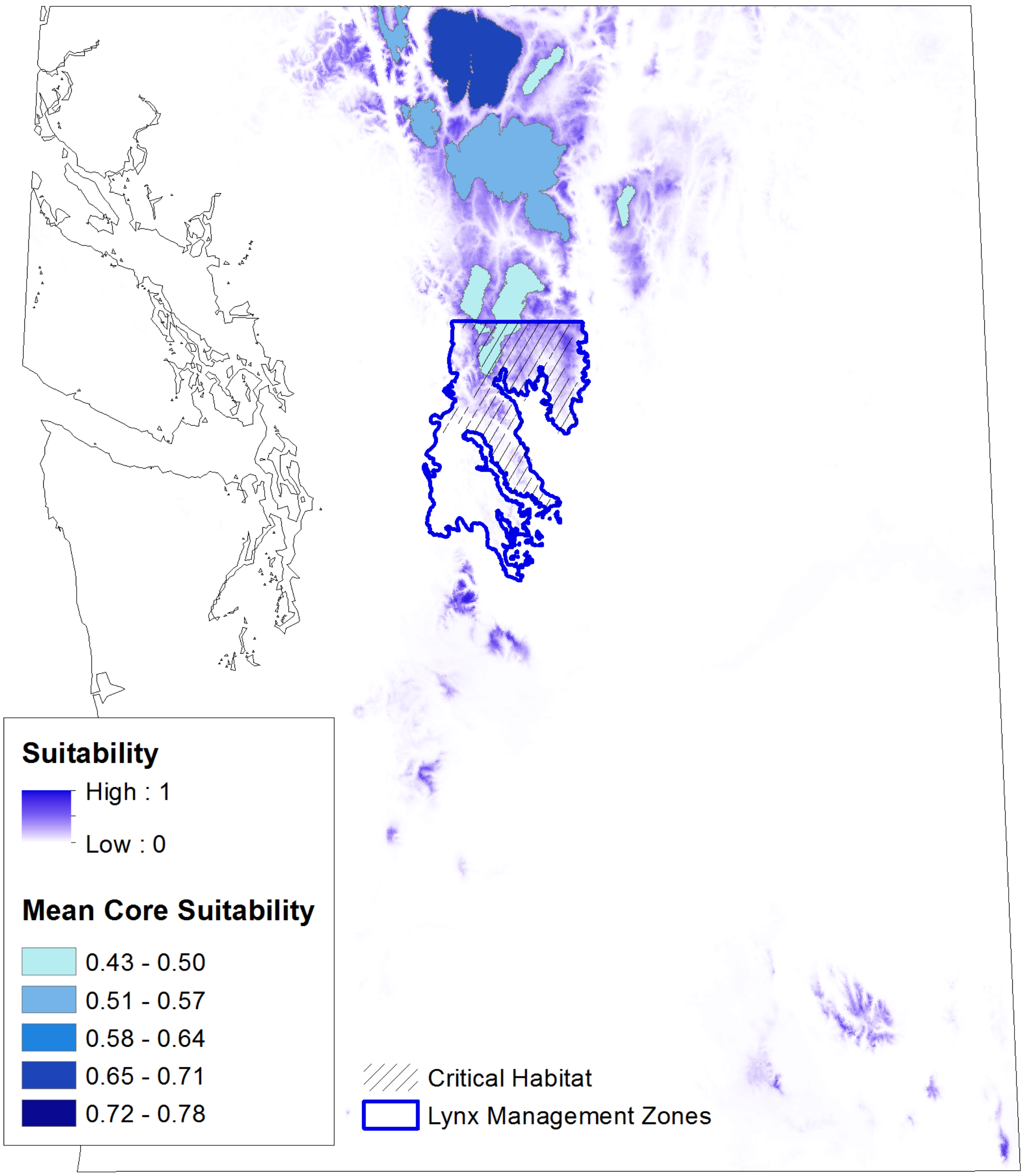


Figure C.7. Projection of *Lynx canadensis* habitat suitability and core areas for the 2020s under the CanESM2 RCP 8.5 climate scenario. Core areas (solid colors) are superimposed over the gradient of projected habitat suitability. Lynx critical habitat (hatch) and the Okanogan Lynx Management Zone (blue outline) are shown for comparison. RCP = Representative Concentration Pathway.

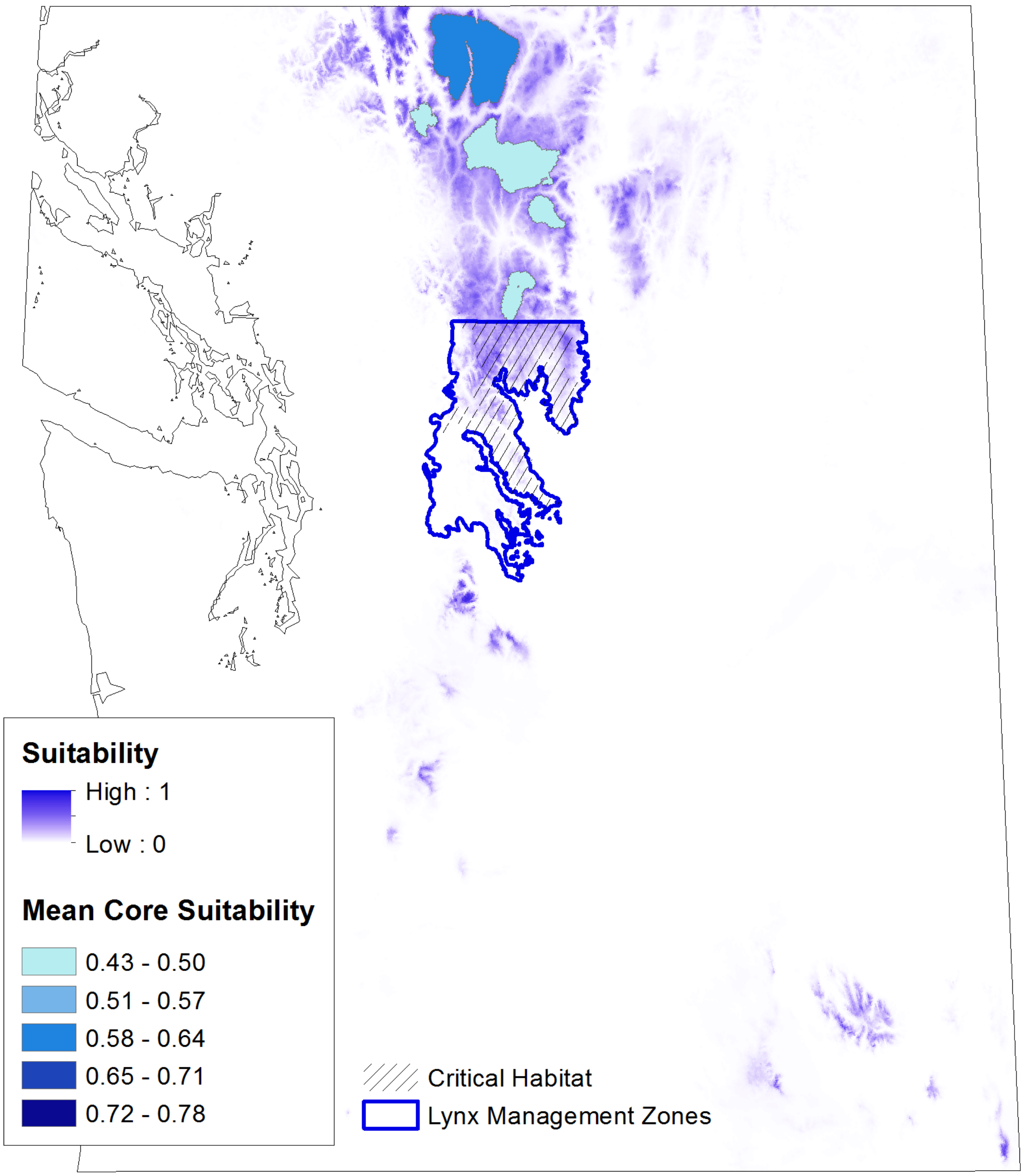


Figure C.8. Projection of *Lynx canadensis* habitat suitability and core areas for the 2050s under the CCSM4 RCP 4.5 climate scenario. Core areas (solid colors) are superimposed over the gradient of projected habitat suitability. Lynx critical habitat (hatch) and the Okanogan Lynx Management Zone (blue outline) are shown for comparison. RCP = Representative Concentration Pathway.

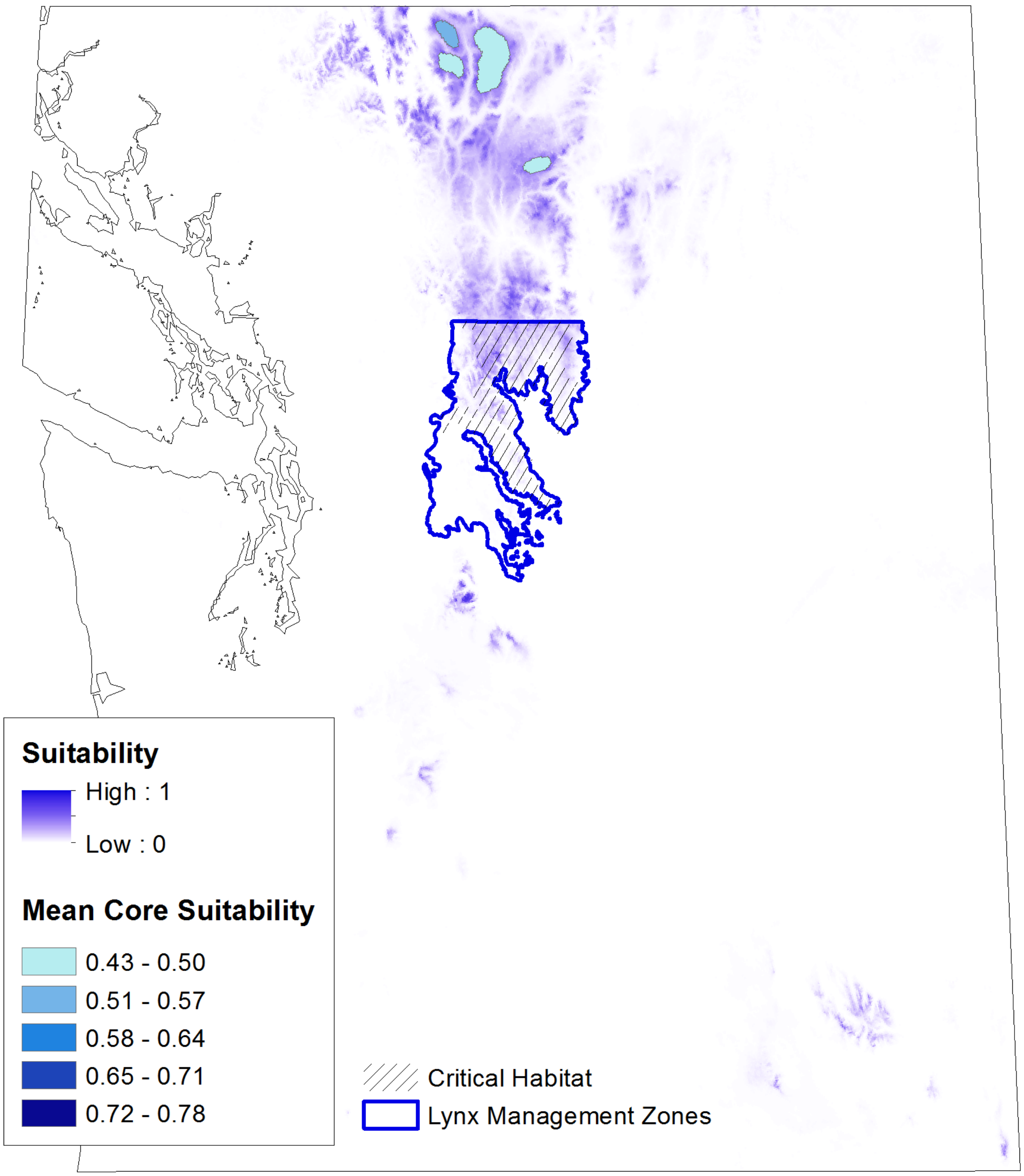


Figure C.9. Projection of *Lynx canadensis* habitat suitability and core areas for the 2050s under the CCSM4 RCP 8.5 climate scenario. Core areas (solid colors) are superimposed over the gradient of projected habitat suitability. Lynx critical habitat (hatch) and the Okanogan Lynx Management Zone (blue outline) are shown for comparison. RCP = Representative Concentration Pathway.

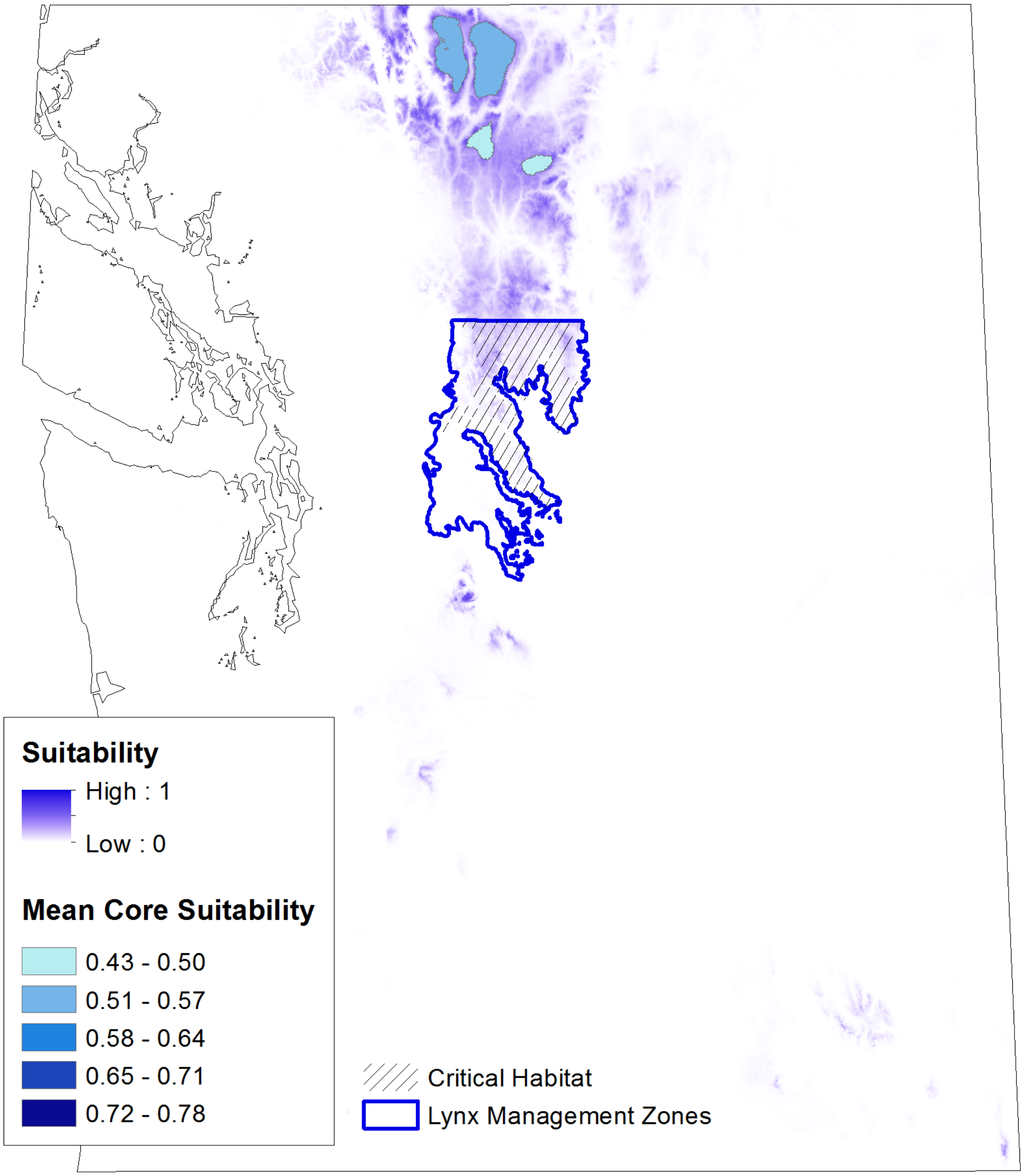


Figure C.10. Projection of *Lynx canadensis* habitat suitability and core areas for the 2050s under the CNRM-CM5 RCP 4.5 climate scenario. Core areas (solid colors) are superimposed over the gradient of projected habitat suitability. Lynx critical habitat (hatch) and the Okanogan Lynx Management Zone (blue outline) are shown for comparison. RCP = Representative Concentration Pathway.

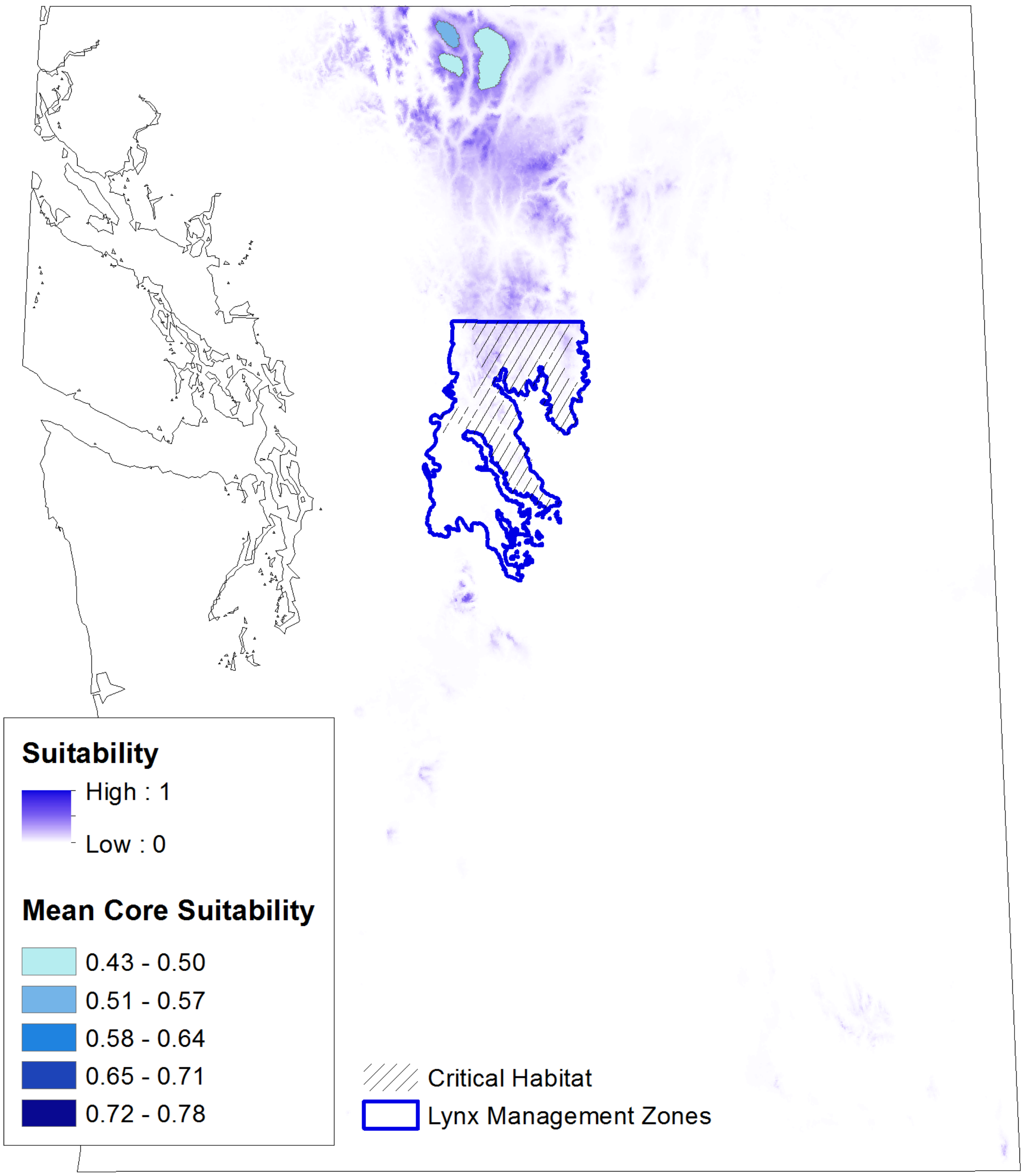


Figure C.11. Projection of *Lynx canadensis* habitat suitability and core areas for the 2050s under the CNRM-CM5 RCP 8.5 climate scenario. Core areas (solid colors) are superimposed over the gradient of projected habitat suitability. Lynx critical habitat (hatch) and the Okanogan Lynx Management Zone (blue outline) are shown for comparison. RCP = Representative Concentration Pathway.

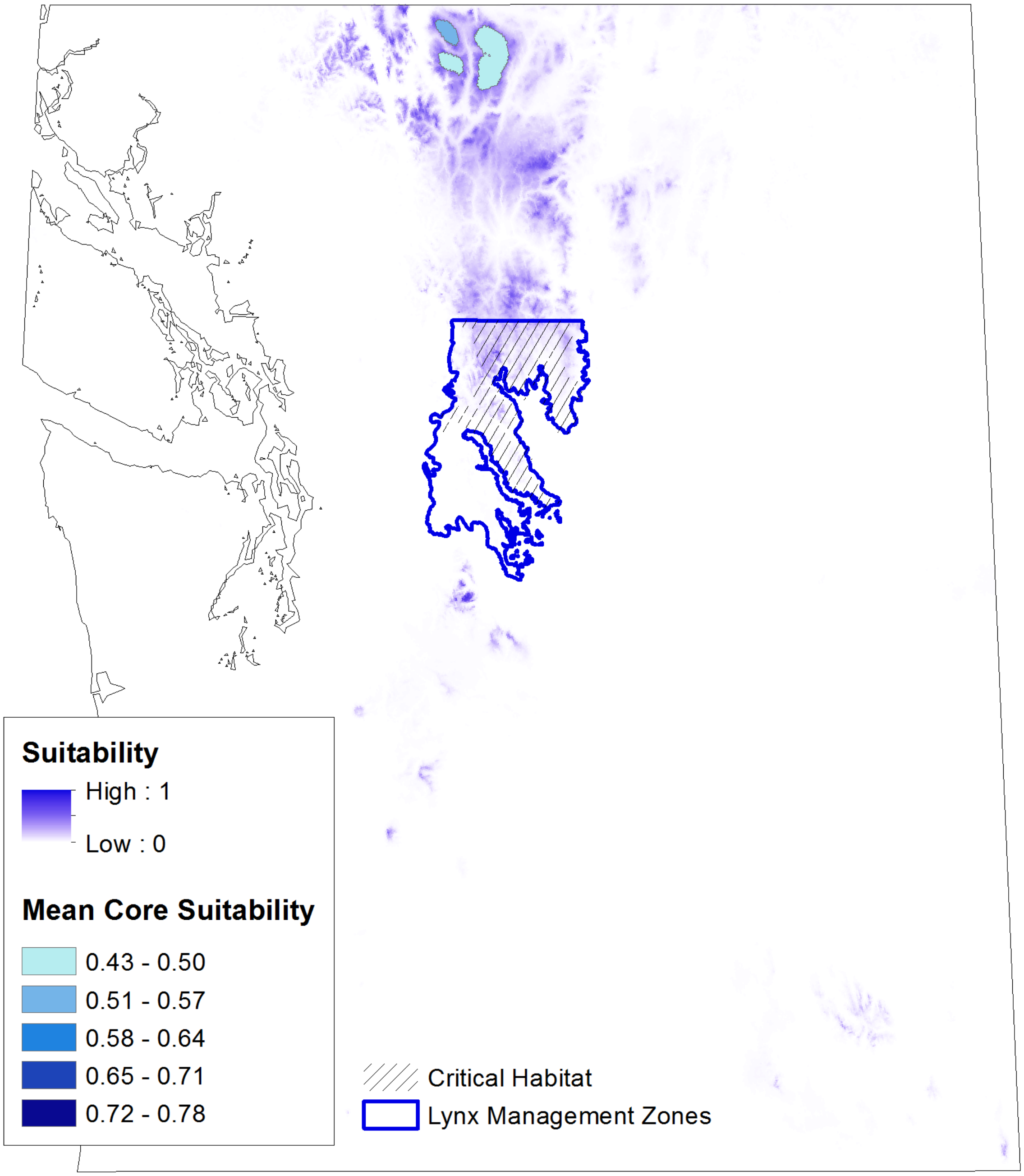


Figure C.12. Projection of *Lynx canadensis* habitat suitability and core areas for the 2050s under the CanESM2 RCP 4.5 climate scenario. Core areas (solid colors) are superimposed over the gradient of projected habitat suitability. Lynx critical habitat (hatch) and the Okanogan Lynx Management Zone (blue outline) are shown for comparison. RCP = Representative Concentration Pathway.

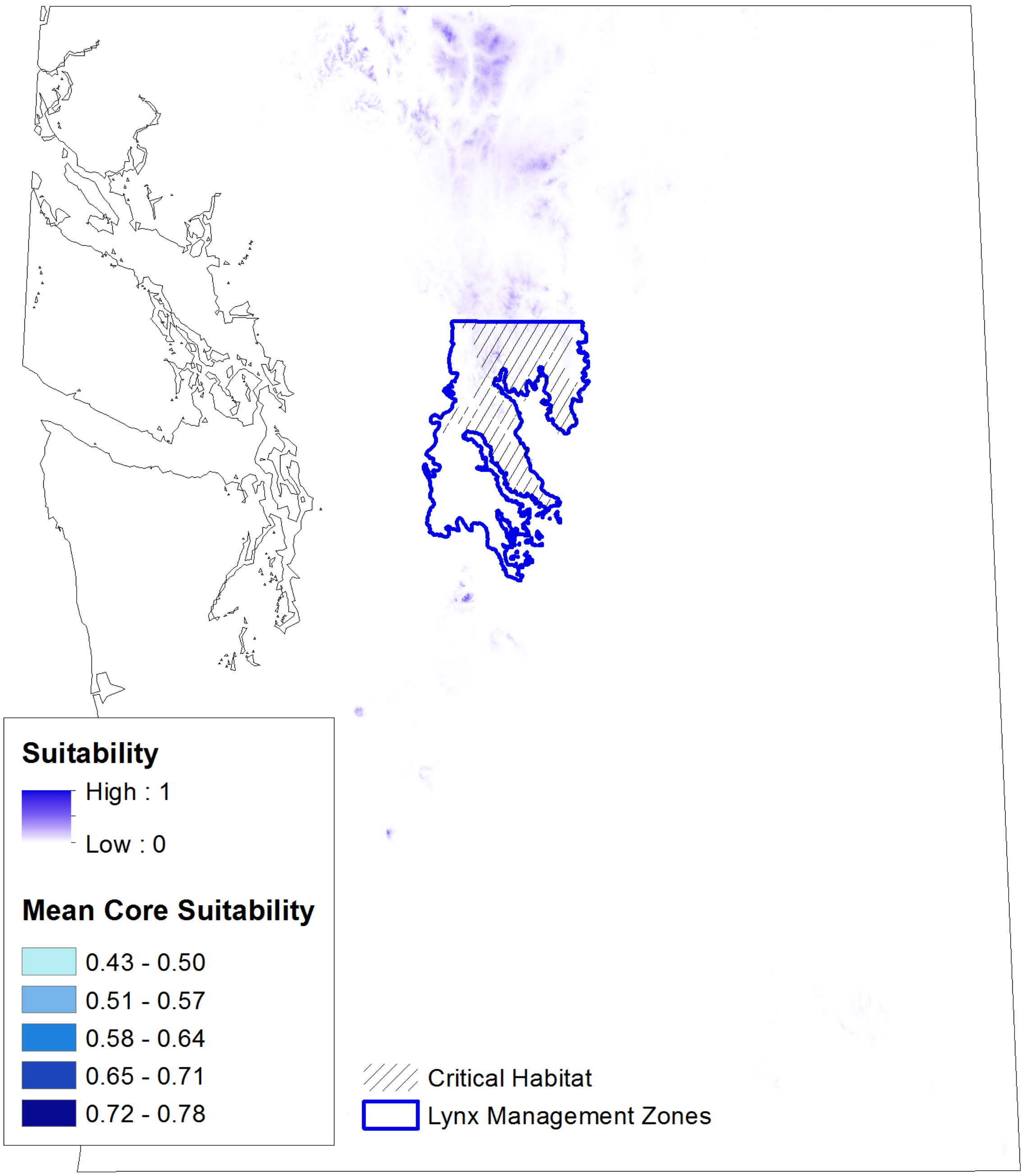


Figure C.13. Projection of *Lynx canadensis* habitat suitability and core areas for the 2050s under the CanESM2 RCP 8.5 climate scenario. Core areas (solid colors) are superimposed over the gradient of projected habitat suitability. Lynx critical habitat (hatch) and the Okanogan Lynx Management Zone (blue outline) are shown for comparison. RCP = Representative Concentration Pathway.

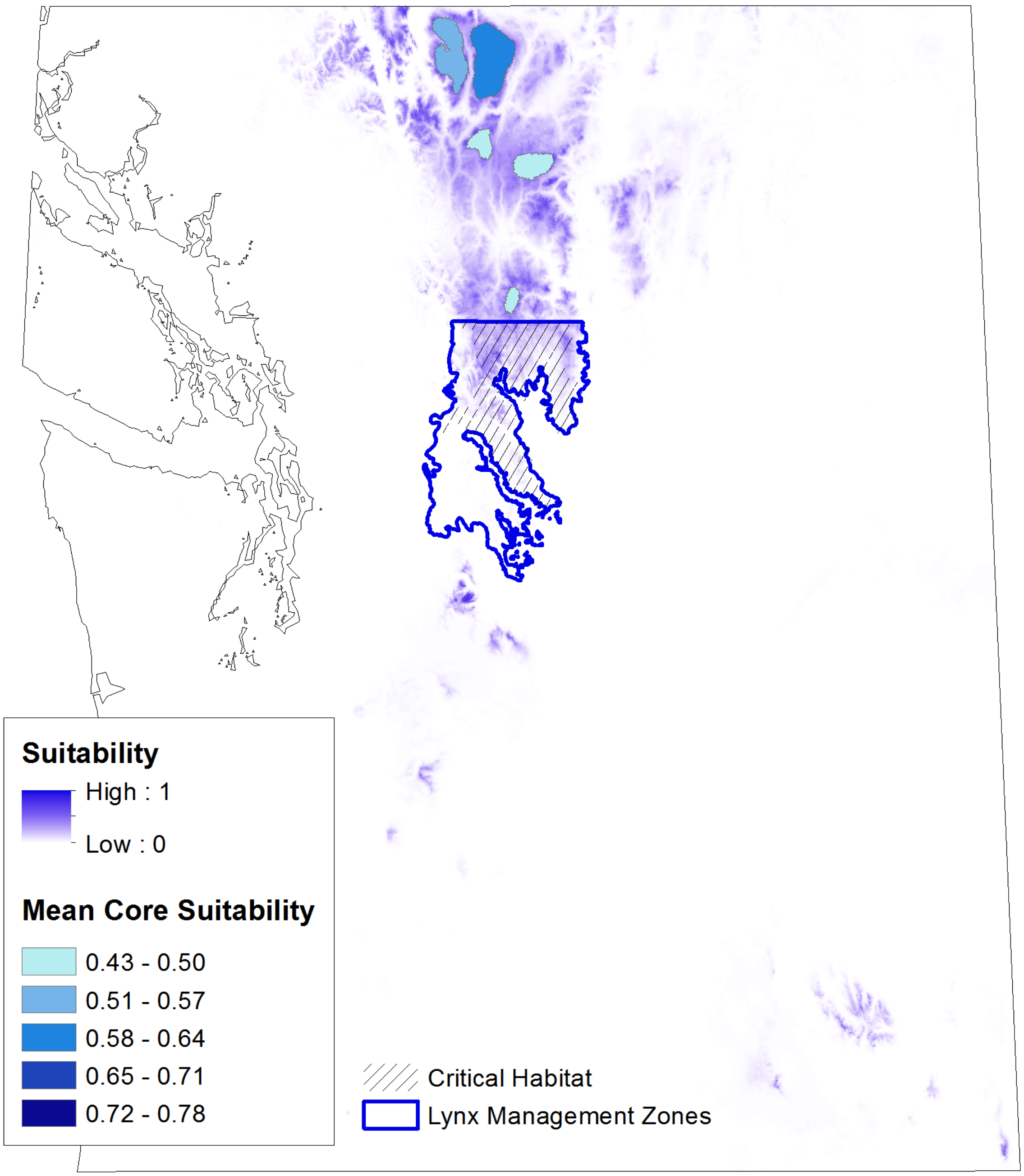


Figure C.14. Projection of *Lynx canadensis* habitat suitability and core areas for the 2080s under the CCSM4 RCP 4.5 climate scenario. Core areas (solid colors) are superimposed over the gradient of projected habitat suitability. Lynx critical habitat (hatch) and the Okanogan Lynx Management Zone (blue) are shown for comparison. RCP = Representative Concentration Pathway.

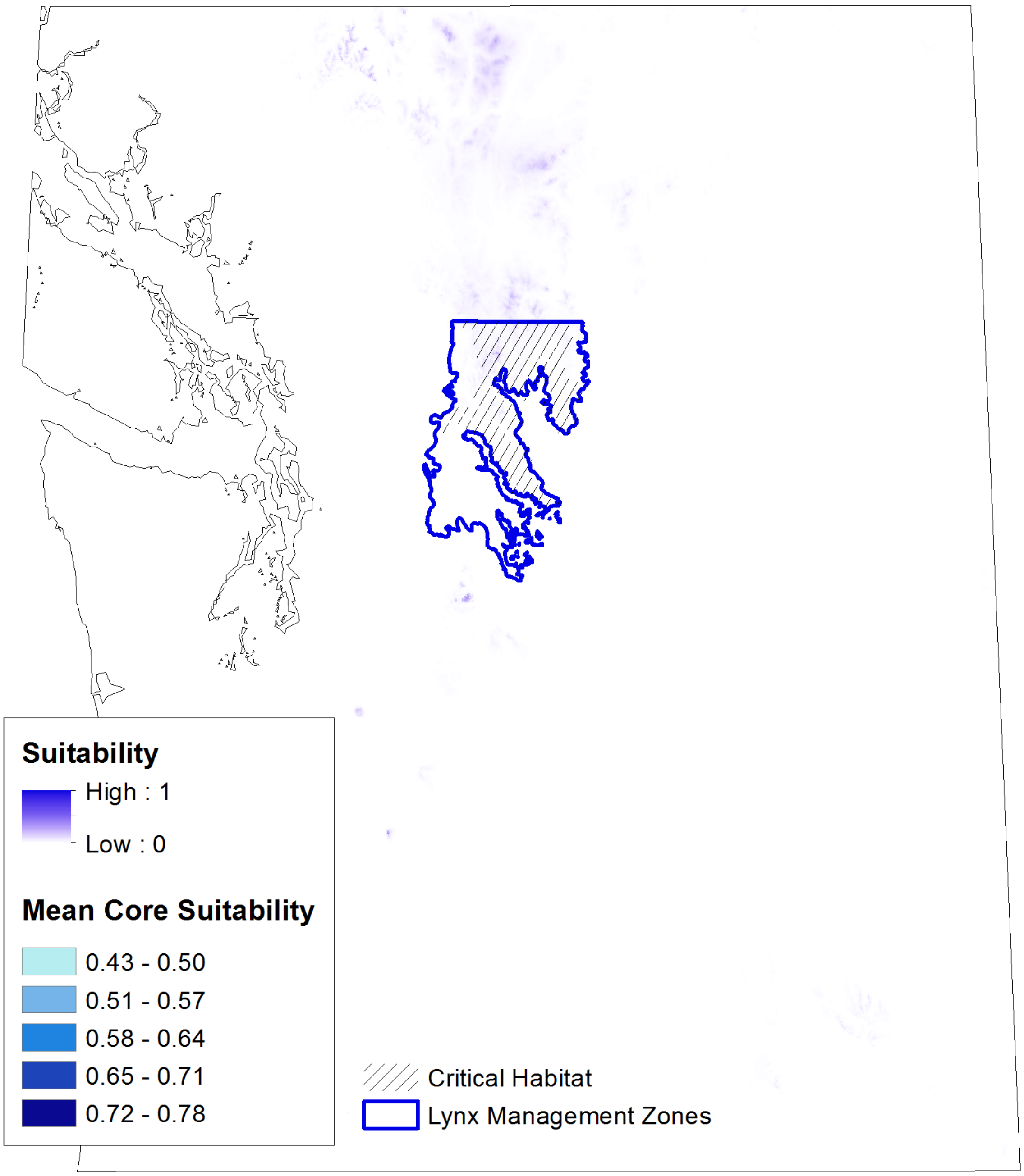


Figure C.15. Projection of *Lynx canadensis* habitat suitability and core areas for the 2080s under the CCSM4 RCP 8.5 climate scenario. Core areas (solid colors) are superimposed over the gradient of projected habitat suitability. Lynx critical habitat (hatch) and the Okanogan Lynx Management Zone (blue outline) are shown for comparison. RCP = Representative Concentration Pathway.

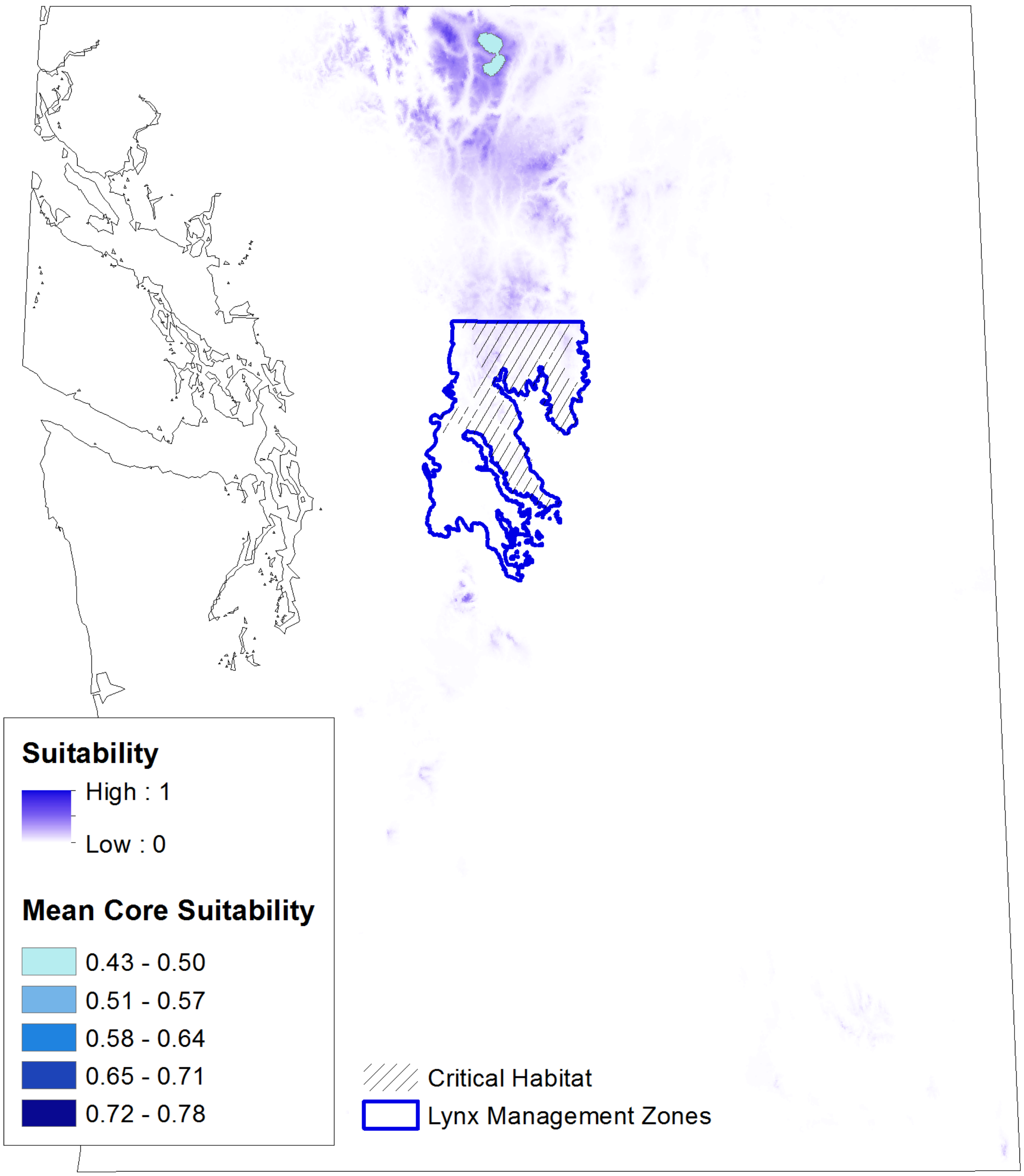


Figure C.16. Projection of *Lynx canadensis* habitat suitability and core areas for the 2080s under the CNRM-CM5 RCP 4.5 climate scenario. Core areas (solid colors) are superimposed over the gradient of projected habitat suitability. Lynx critical habitat (hatch) and the Okanogan Lynx Management Zone (blue outline) are shown for comparison. RCP = Representative Concentration Pathway.

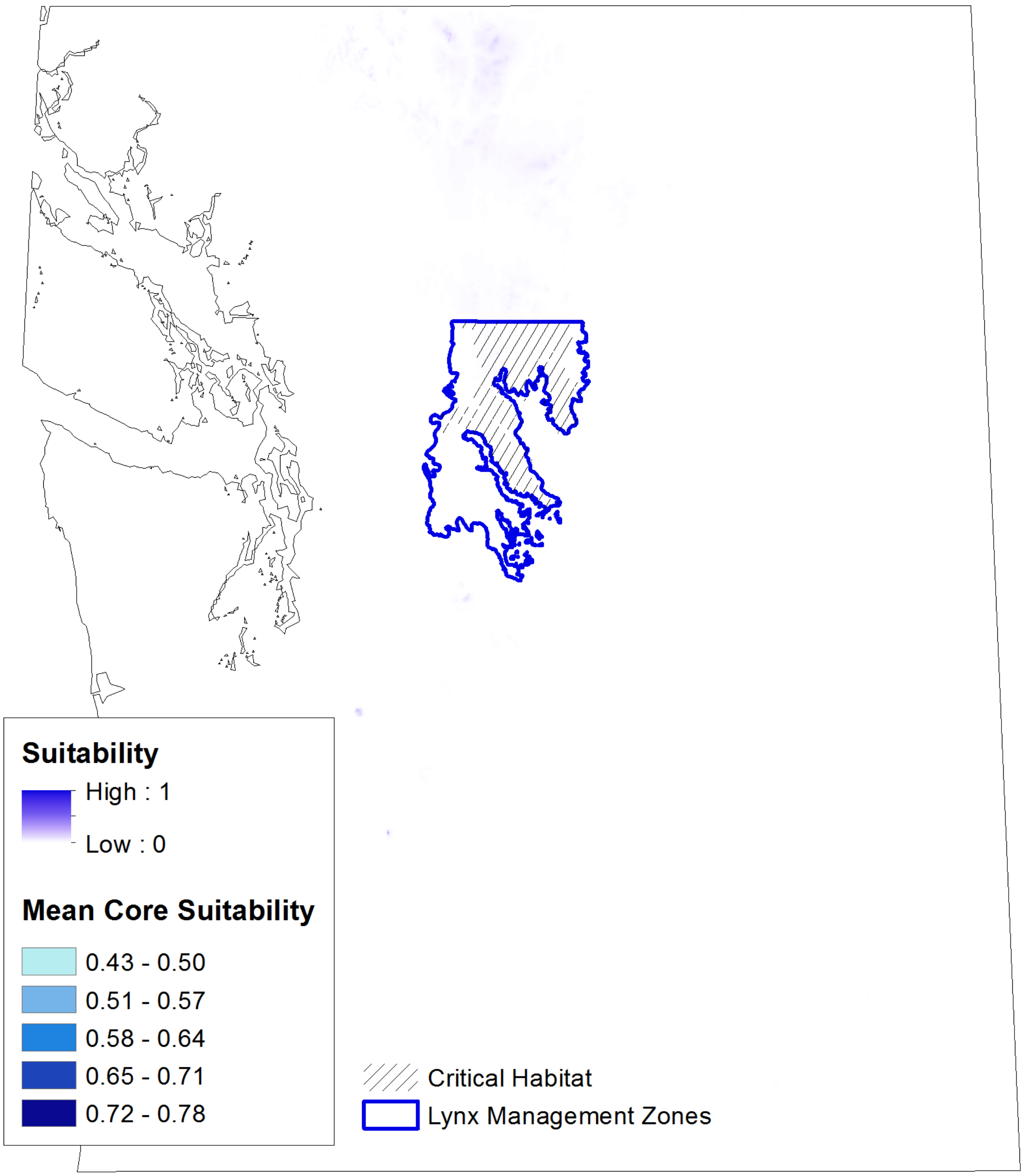


Figure C.17. Projection of *Lynx canadensis* habitat suitability and core areas for the 2080s under the CNRM-CM5 RCP 8.5 climate scenario. Core areas (solid colors) are superimposed over the gradient of projected habitat suitability. Lynx critical habitat (hatch) and the Okanogan Lynx Management Zone (blue outline) are shown for comparison. RCP = Representative Concentration Pathway.

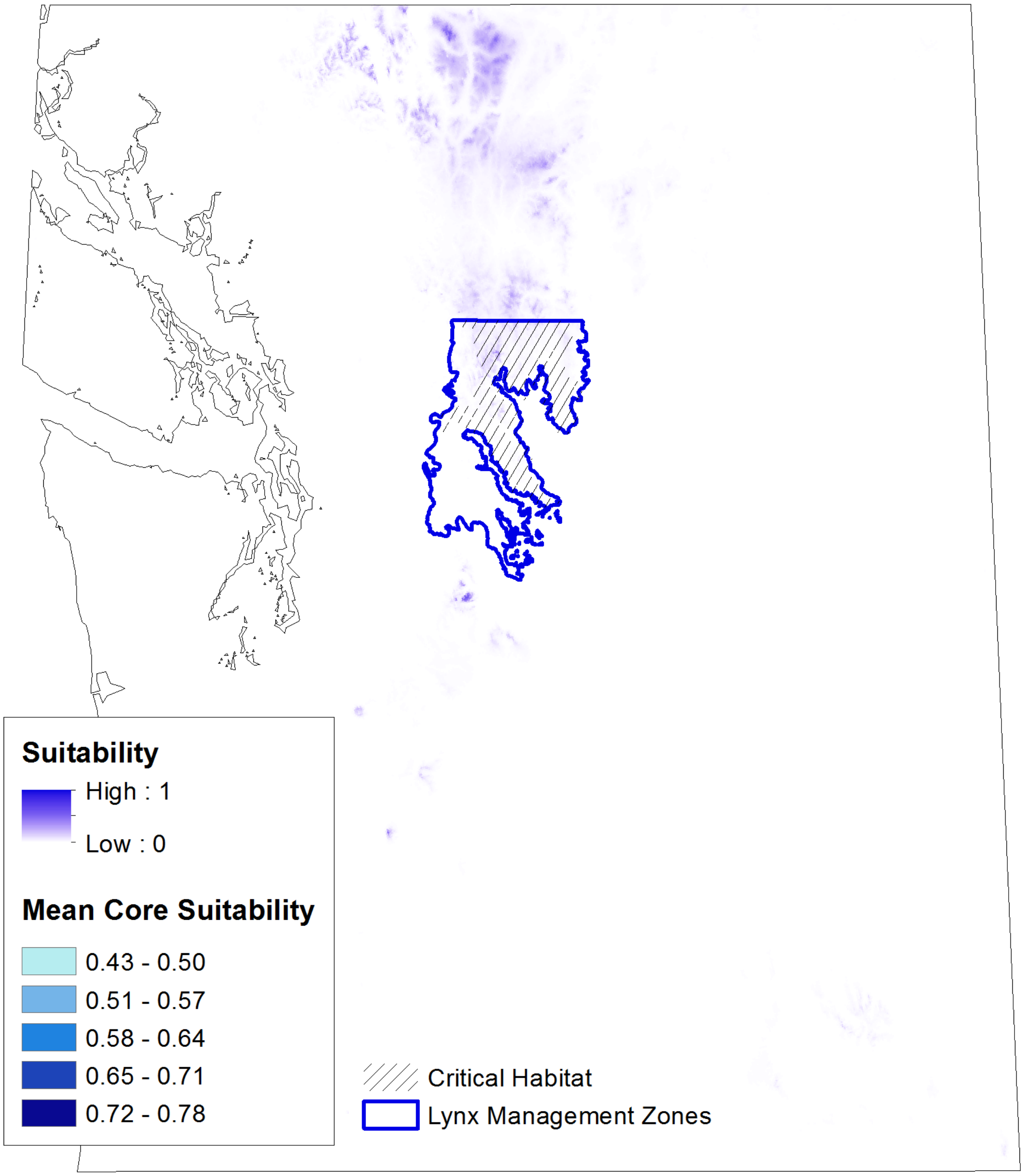


Figure C.18. Projection of *Lynx canadensis* habitat suitability and core areas for the 2080s under the CanESM2 RCP 4.5 climate scenario. Core areas (solid colors) are superimposed over the gradient of projected habitat suitability. Lynx critical habitat (hatch) and the Okanogan Lynx Management Zone (blue outline) are shown for comparison. RCP = Representative Concentration Pathway.

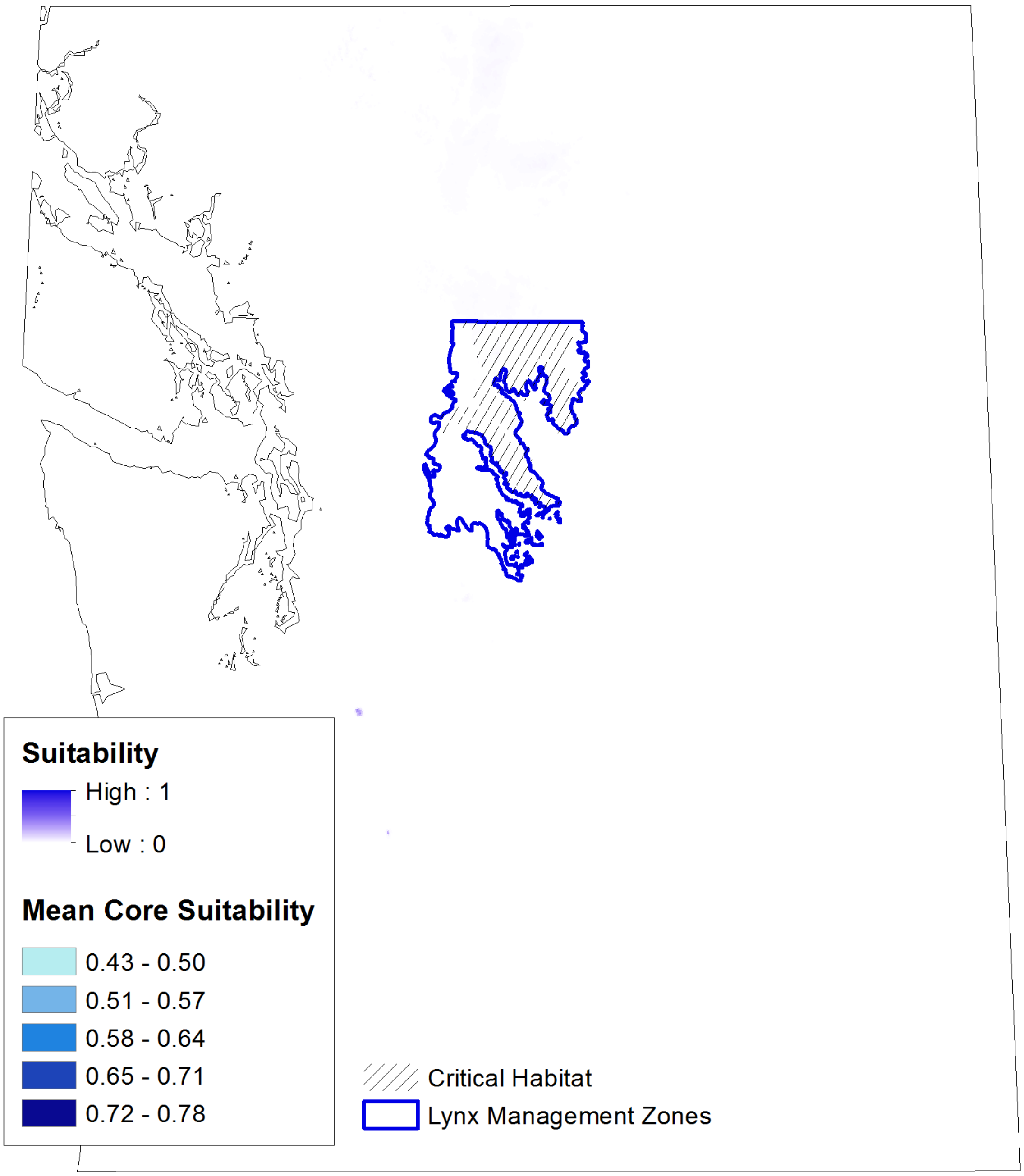


Figure C.19. Projection of *Lynx canadensis* habitat suitability and core areas for the 2080s under the CanESM2 RCP 8.5 climate scenario. Core areas (solid colors) are superimposed over the gradient of projected habitat suitability. Lynx critical habitat (hatch) and the Okanogan Lynx Management Zone (blue outline) are shown for comparison. RCP = Representative Concentration Pathway.

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